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THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

COMPARISON OF THE CRANE FLIES (DIPTERA: TIPULIDAE) OF TWO WOODLANDS IN EASTERN KANSAS, WITH A KEY TO THE ADULT CRANE FLIES OF EASTERN KANSAS

By

CHEN-WEN YOUNG

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Comparison of the Crane Flies (Diptera: Tipulidae) of Two Woodlands in Eastern Kansas, With a Key to the Adult Crane Flies of Eastern Kansas[1]

Chen-Wen Young

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1. Contribution no. 1658 from the Department of Entomology, University of Kansas, Lawrence, Kansas 66045. This investigation was supported in part by University of Kansas General Research allocation #3677-x038, Prof. George W. Byers, principal investigator.

ABSTRACT

Data on geographical and ecological distribution have been compiled for the 95 species of crane flies found in two natural areas in northeastern Kansas, the Breidenthal Reserve and the Natural History Reservation of the University of Kansas. These distributions correlate well with various major plant communities, or with specific habitats. The ranges of several species are extended significantly westward. New records for species not previously recorded within 500 miles of Lawrence, Kansas, include: *Nephrotoma alterna, Tipula* (*L.*) *perlongipes, Limonia* (*D.*) *haeretica, Dicranoptycha elsa, D. megaphallus, D. septemtrionis, Gonomyia* (*L.*) *manca, Ormosia arcuata, O. ingloria, Tasiocera* (*D.*) *ursina* and *Molophilus pubipennis.*

INTRODUCTION

This paper reports the results of intensive field studies of the crane fly populations of two natural areas belonging to the University of Kansas, the Natural History Reservation and the Breidenthal Reserve. The primary objective was to determine and compare what species comprise the crane fly faunas of the two reservations, and to ascertain their relative abundance, seasonal distribution, and habitat correlations. When species seemed to be excluded from one of the reservations, the supposedly appropriate habitat was examined closely in an attempt to determine what ecological differences between the two reservations might account for the absence.

The combined fauna was examined to determine the probable origins of eastern Kansas crane flies. Comparative data were obtained from similar studies made by J. Speed Rogers (1942) at the George Reserve in southeastern Michigan, and B. A. Foote (1956) in Delaware County, Ohio. Overall range data were obtained from *A Catalog of the Diptera of America North of Mexico* (Stone, et al., 1965). Included are a brief account of the habitat, abundance, etc., of each species encountered and a taxonomic key to local species.

Until this study, none of the following species had been reported within a 500 mile radius of Lawrence, Kansas: *Nephrotoma alterna, Tipula* (*L.*) *perlongipes, Limonia* (*D.*) *haeretica, Dicranoptycha elsa, D. megaphallus, D. septemtrionis, Gonomyia* (*L.*) *manca, Ormosia arcuata, O. ingloria, Tasiocera* (*D.*) *ursina,* and *Molophilus pubipennis.*

GENERAL FEATURES OF THE STUDY AREAS

EASTERN KANSAS

Kansas is at the geographic center of the contiguous continental United States. Except for its hilly eastern part, it is a plain sloping gradually downward to the east and is usually regarded as a prairie state. However, within its borders there are approximately 1,358,000 acres of forest, mostly in the eastern hills, where edaphic conditions and an annual precipitation of approximately 34.75 inches are adequate for upland forests. Some expansion of forests westward has followed agricultural activity and the cessation of prairie fires. Eastern Kansas is in a transition zone between the eastern forests and the central plains.

DOUGLAS COUNTY

Douglas County is in northeastern Kansas. Its main topographic features are the Kansas and Wakarusa river valleys, draining eastward, and uplands formed by differential erosion of the nearly horizontal beds of limestone, shale and sandstone. In the eastern part of the county, plains have

developed on glacial deposits. The climate is humid, with cold winters and warm to hot summers, three-fourths of the annual precipitation falling during the warm season from April through September. Most of the county is now agricultural land.

The Breidenthal Reserve

The Breidenthal Reserve (Baldwin Woods) comprises 110 acres of mixed broad-leaf deciduous forest in southern Douglas County, about 2 miles north of Baldwin City and 15 miles southeast of Lawrence. It includes part of the steep slope along the south side of the Wakarusa River Valley and is drained by Coal Creek. The area is mostly oak-hickory forest, with variation depending upon the locality and drainage. The creek is narrowly bordered with flood-plain species of trees. Low oak-hickory forest occurs regularly on the moderately mesic hillside and north-facing slopes, while drier, upland, oak-hickory forest grows on the south-facing slopes.

The University of Kansas Natural History Reservation

The University of Kansas Natural History Reservation is at the north edge of the Kansas River Valley in northern Douglas County, about 5 miles northeast of Lawrence. Two intermittent brooks drain its 590 acres, one in the northwestern part, the other in the southeastern part. A pond, formed by damming of the northwestern brook, has a small swamp around its northeastern edge. Most of the Reservation supports broaf-leaf deciduous forest, with scattered grassy openings. This area had been heavily grazed before it became the Reservation in 1948, its present vegetation is still in a successional state.

CRANE FLY HABITATS

Some adult crane flies in the two study areas are restricted to a single type of habitat, while others are widespread. Humidity and temperature affect flight and other activities, so that distribution of adult flies only approximates that of the larvae; yet there is usually a close correlation. Six, general, crane fly habitats exist in the study areas. Following the description of each, below, is a list of the species of crane flies recorded from it.

Bottomland Forest

The Breidenthal Reserve has bottomland forest along Coal Creek that contains mixed species of oak and hickory (*Quercus macrocarpa, Q. alba, Q. rubra, Carya ovata, C. cordiformis*), sycamore (*Platanus occidentialis*), and American elm (*Ulmus americana*). The shrub layer is poorly developed. The vernal herbaceous flora is very well developed. Undergrowth includes nettle (*Urtica procera*), and jewelweed (*Impatiens capensis*), with sparse patches of grass. There is sporadic flooding in spring and early summer, and a dry season in late summer. This is a mesic area. Crane flies present are: *Dolichopeza tridenticulata, Nephrotoma alterna, N. euceroides, N. macrocera, N. polymera, Tipula trivittata, T. duplex, T. flavoumbrosa, T. mallochi, T. ultima, T. furca, T. sayi, T. strepens, Limonia fallax, L. globithorax, L. tristigma, L. divisa, L. pudica, L. domestica, Helius flavipes, Dicranoptycha septemtrionis, D. tigrina, Epiphragma fasciapennis, E. solatrix, Pilaria tenuipes, Cladura flavoferruginea, Gnophomyia tristissima, Gonomyia florens, G. manca, G. sulphurella, Erioptera cana, E. vespertina, E. caloptera, E. needhami, E. armata, Ormosia romanovichiana, Tasiocera arsina, Molophilus pubipennis.*

Grassland

Grasslands in which Tipulidae occur in the two study areas are ecotone areas between small grassy fields and the edge of woods. These are too dry for most crane

flies, but some species whose larval stages feed on the roots of certain herbaceous plants growing in the grassland occur as adults in the ecotone of the grassland and woods. Such species are: *Nephrotoma ferruginea, Tipula bicornis, T. flavibasis, T. triplex, T. paterifera, T. ultima, Erioptera cana, E. septemtrionis.*

Oak-Hickory Forests

The oak-hickory forests of the Breidenthal Reserve are in stable climax, dominated by shagbark hickory (*Carya ovata*), chestnut oak (*Quercus muehlenbergii*), red oak (*Quercus rubra*), and red elm (*Ulmus rubra*). Understory trees include ironwood (*Ostrya virginiana*), red mulberry (*Morus rubra*), redbud (*Cercis canadensis*), and pawpaw (*Asimina triloba*). The undergrowth is generally open with some growth of poison ivy (*Rhus radicans*), wild gooseberry (*Ribes missouriense*) and buckbrush (*Symphoricarpos orbiculatus*). Leaf litter and, beneath it, leaf mold are present over most of the level areas and gentler slopes. Fallen trees and decaying limbs there are usually too dry to harbor most crane fly larvae. Mats of dry mosses are scattered on the ground surface. Oak-hickory forests are too dry for most crane flies; few species are present: *Nephrotoma ferruginea, Tipula disjuncta, T. duplex, T. fuliginosa, T. perlongipes, T. tuscarora, T. stonei, Limonia triocellata, L. domestica, Dicranoptycha elsa, D. megaphallus, D. septemtrionis, Cladura flavoferruginea, Gonomyia subcinerea, Erioptera cana.*

Streams

The small, intermittent brooks on the Natural History Reservation ordinarily flow only in spring and early summer. They dry up quickly by mid-summer, although pools may persist in the stream beds for several weeks after flow has ceased. Coal Creek in the Breidenthal Reserve flows from early spring until August, and has small pools which persist through September. A few, small, ravine tributaries feed into it in spring. Several species of crane flies inhabit the banks and beds of these streams. Their larvae probably occur in submerged, rotten, tree branches, and in the algae or mosses covering rocks in and along the streams. These are: *Dolichopeza obscura, D. tridenticulata, D. walleyi, Tipula furca, T. strepens, Limonia rara, L. annulata, L. humidicola, L. bryanti, L. domestica, L. lecontei, L. communis, Erioptera armata, Ormosia romanovichiana, Tasiocera ursina, Molophilus pubipennis.*

Swamp

The artificial pond on the Natural History Reservation supports a small swamp of recent origin around its northeastern edge. Tree species common here are willows (*Salix* spp.), American elm (*Ulmus americana*), and honey locust (*Gleditsia triacanthos*). No shrub stratum is developed. The water rises and covers most of the area during spring and early summer. At the low-water stage the area is almost completely covered by smartweeds (*Polygonum hydropiper*). The moist-to-wet soil is the preferred habitat for the larvae of several species of crane flies. They are: *Nephrotoma alterna, N. eucera, N. euceroides, N. macrocera, N. polymera, Tipula ignobilis, T. ultima, T. furca, T. strepens, T. tricolor, Limonia tristigma, L. pudica, L. domestica, Dicranoptycha pallida, Epiphragma fasciapennis, E. solatrix, Pilaria imbecilla, P. quadrata, P. tenuipes, Atarba picticornis, Teucholabis lucida, Erioptera vespertina, E. caliptera, E. parva, E. graphica, Tasiocera ursina, Molophilus hirtipennis, M. pubipennis.*

Valley Hillside Woods

In the Breidenthal Reserve, low oak-hickory forests grow on well-drained soils

on the gently sloping, moist to mesic, north-facing hillsides. Ground cover species include tick trefoil (*Desmodium glutinosum*), Virginia creeper (*Parthenocissus quinquefolia*), and mayapple (*Podophyllum peltatum*).

The valleys in the Natural History Reservation are wooded with American elm (*Ulmus americana*), honey locust (*Gleditsia triacanthos*), black walnut (*Juglans nigra*), and osage orange (*Maclura pomifera*), with dogwood (*Cornus drummondii*) and wild plum (*Prunus americana*) forming the understory. Shrubs present are poison ivy (*Rhus radicans*), wild gooseberry (*Ribes missouriense*), buckbrush (*Symphoricarpos orbiculatus*), and brambles (*Rubus* spp.). The herb stratum is sparsely developed, only where the tree canopy has been broken.

In the spring, these two previously described habitats are moderately mesic. Fallen tree trunks in various stages of decomposition, and soil covered by damp and friable humus form a habitat for larvae of several species of crane flies. These include the following: *Dolichopeza tridenticulata, D. walleyi, Nephrotoma alterna, N. euceroides, N. macrocera, N. virescens, Tipula trivittata, T. dietziana, T. dorsimacula, T. duplex, T. flavoumbrosa, T. fuliginosa, T. mallochi, T. morrisoni, T. translucida, T. integra, T. unimaculata, Limonia cinctipes, L. fallax, L. immatura, L. divisa, L. haeretica, L. immodestoides, L. liberta, L. pudica, L. domestica, Dicranoptycha elsa, D. megaphallus, D. pallida, D. sobrina, Epiphragma fasciapennis, E. solatrix, Pseudolimnophila contempta, Pilaria tenuipes, Atarba picticornis, Elephantomyia westwoodi, Cladura flavoferruginea, Teucholabis complexa, Gonomyia subcinerea, Erioptera cana, Ormosia ingloria.*

METHODS

This report is based largely upon field observations and collections made in the two study areas described. Collections were made from May 1974 to September 1975 as often as time permitted. Throughout the peak-emergence periods of adult flies, collections were conducted on alternate days at the Breidenthal Reserve and the Natural History Reservation. At first all varieties of habitats were searched. Later, searches were concentrated on several specific sites believed to represent the principal types of crane fly habitats.

Net sweeping was the basic method of collecting. All possible hiding places were explored with the net. Specimens were taken either at their resting site, or in the air as they fled. No more than 20 specimens per species were captured at each habitat on each trip. All flies caught by net were mounted.

In the spring of 1975, a Malaise trap was set in the bottomland along the creek near the mouth of a ravine on the Breidenthal Reserve; another was set in the swamp woods at the Natural History Reservation. Each was checked at five-day intervals, and all flies trapped were kept in alcohol.

Ecological information recorded about the specimens included weather conditions at time of collection, type of habitat with which flies were associated, microhabitat where flies were taken, relative abundance of each species, data on behavior of the flies (when appropriate), and other noteworthy details. Larvae were taken and rearing data were obtained whenever possible.

SEASONAL DISTRIBUTION

In eastern Kansas adult crane flies usually emerge during wet seasons. At both reservations their appearance begins with *Erioptera cana* in late March, reaches a peak period in May and early June, and ends with *Cladura flavoferruginea* in mid-October. Winter crane flies, *Chionea stoneana,* appear in January.

Many species have single, short, clear-cut adult seasons and can be classified as univoltine, spring, summer, or autumnal forms, according to the flight periods of the adults. However, some species complete two generations per year and have two flight periods. Temporal disjunction between generations is either total or partial. For example, adults of *Tipula* (*Yamatotipula*) *furca* first emerge in late April, disappear in summer, and recur in early September, while adults of *Nephrotoma macrocera* can be found on the wing from May until September. Multivoltine species such as *Erioptera cana,* fly as adults from March to October. Temporary fluctuations in environmental factors markedly affect the number of generations during the summer.

Table 1 summarizes seasonal distribution of adults. In the table, each month is divided into ten-day intervals, and the symbols 'X', 'x', and '–' are used to indicate, respectively, the peak period (common), the intermediate period (numerous), and the period of least abundance (rare) within the species. At the right, local occurrence of the species is summarized; Br.—Breidenthal Reserve; and NH.—Natural History Reservation.

RELATIVE ABUNDANCE OF SPECIES

Each major habitat was visited for about half an hour on each collecting trip. Categories indicating relative abundance and distributional pattern were modified from Rogers (1942). Abundance is expressed as the number of flies that could be caught per half-hour: abundant—more than 20; common—10-20; numerous—fewer than 10; rare—one only. Ecological distribution: widespread—present in four to six habitats; general—continuous in two adjacent habitats; local—restricted to one habitat.

ANNOTATED LIST OF SPECIES

In this annotated list, the brief account of each species includes its habitat, flight period, relative abundance, and previously known range. Br.—Breidenthal Reserve; NH.—Natural History Reservation.

1. *Dolichopeza* (*Oropeza*) *obscura* (Johnson)

Br. 1975; May 22-June 10. Also taken by G. W. Byers on August 30, 1961; bivoltine.

Only three specimens were taken in 1975, found associated with other species of *Dolichopeza* under a wooden culvert in a woodland ravine.

Previously known range: Alberta to Nova Scotia, southward to Arkansas and Florida.

2. *Dolichopeza* (*Oropeza*) *tridenticulata* Alexander

Br. NH. 1974-1975; May 23-June 26, and a single male on August 7, 1974; bivoltine.

Common, to locally abundant in well-shaded, mesic situations, such as beneath a wooden culvert, under protruding rocks along stream bed, and in the shade of upturned, shallow, tree roots. Usually the flies were found hanging from the roof of their nesting places with the hind legs pendant.

Previously known range: Manitoba to Quebec and Maine, southward to Missouri and Georgia.

3. *Dolichopeza* (*Oropeza*) *walleyi* (Alexander)

Br. NH. 1974-1975; May 22-June 17, and July 16-August 7; bivoltine.

This species is common in May and June, but rare in August. Most specimens were from wet, well-shaded places. One rich collecting spot was the wooden culvert in Br. Adults were usually taken where *tridenticula* was also common, or resting in low shrubs and herbs.

TABLE 1

Summary of Seasonal Distribution of Adults

No.	Species	Mar. 1	2	3	Apr. 1	2	3	May 1	2	3	June 1	2	3	July 1	2	3	Aug. 1	2	3	Sept. 1	2	3	Oct. 1	2	3	Br.	NH.
1.	Dolichopeza (O.) obscura (Johnson)								-	-	-	-														x	
2.	Dolichopeza (O.) tridenticulata Alex.								-	-	x	X	X	x	-											x	x
3.	Dolichopeza (O.) wallevi (Alex.)								-	x	x	X	x	-	-	-	-	-								x	x
4.	Nephrotoma alterna (Walker)								-	x	X	x	x	x	-	-				-						x	x
5.	Nephrotoma eucera (Loew)									-																	x
6.	Nephrotoma euceroides Alex.								-	-	x	X	X	X	x	-										x	x
7.	Nephrotoma ferruginea (Fabr.)	-	-	-	-	-	-	-	-	x	x	x	-							-	-	-	-	x	-	-	x	x
8.	Nephrotoma macrocera (Say)							-	-	-	-	x	x	x	X	X	x	x	-	-	-	-	-	-	-	x	x	x
9.	Nephrotoma polymera (Loew)								-	-	-	x	X	X	x	-										x	x
10.	Nephrotoma virescens (Loew)									-	-	-														x	
11.	Tipula (P.) ignobilis Loew									-	-																x
12.	Tipula (P.) trivittata Say							-	-	x	-															x	x
13.	Tipula (L.) australis Doane							-	-																		x
14.	Tipula (L.) bicornis Forbes							-	x	X	x	-														x	x
15.	Tipula (L.) dietziana Alex.							x	x	-																x	x
16.	Tipula (L.) disjuncta Walker							x	-	-																	x
17.	Tipula (L.) dorsimacula Walker							-	x	x	-															x	x
18.	Tipula (L.) duplex Walker								-	-	x	X	X	X	x	x	-	-	-	-	-	-	-	-	-	x	x
19.	Tipula (L.) flavibasis Alex.									-	-	-	-	-	-	x	-									x	x
20.	Tipula (L.) flavoumbrosa Alex								-	-	x	X	X	x	-											x	x
21.	Tipula (L.) fuliginosa (Say)								-	x	x	-	-													x	x
22.	Tipula (L.) mallochi Alex.								-	x	X	x	x	x	-											x	x
23.	Tipula (L.) morrisoni Alex.									-	-	-	x	-	-											x	x
24.	Tipula (L.) perlongipes Johnson									-	-	-	-	-												x	x
25.	Tipula (L.) species near T. perlongipes									-	-	-	-	-												x	
26.	Tipula (L.) translucida Doane									-	-	-															x
27.	Tipula (L.) triplex Walker								-	x	X	x	-													x	x
28.	Tipula (L.) integra Alex.								-	x	X	x	-	-	-											x	x
29.	Tipula (L.) tuscarora Alex.									-	-	x	-													x	
30.	Tipula (P.) paterifera Alex.																						-	x	-	x	x
31.	Tipula (P.) ultima Alex.																			-	-	-	x	X	x	x	x
32.	Tipula (Tr.) unimaculata Loew)													-	-	x	-	-	-							x	x
33.	Tipula (Tr.) stonei Alex.																				-	x	x	-	-	x	
34.	Tipula (Y.) furca Walker							-	-	x	X	x	-	-	-	-	-	-	-		-	x	-	-	-	x	x

No.	Species	Mar. 1 2 3	Apr. 1 2 3	May 1 2 3	June 1 2 3	July 1 2 3	Aug. 1 2 3	Sept. 1 2 3	Oct. 1 2 3	Br.	NH.
35.	Tipula (T.) sayi Alex.							-		x	
36.	Tipula (Y.) strepens Loew			----xXxx----		- -	-xx-			x	x
37.	Tipula (Y.) tricolor Fabricius			---							x
38.	Tipula (L.) globitarox (O. S.)						---x---			x	
39.	Limonia (L.) rara (O. S.)				--xxx----		-------			x	x
40.	Limonia (L.) tristigma (O. S.)				xXXx--					x	x
41.	Limonia (M.) cinctipes (Say)				---					x	x
42.	Limonia (M.) fallax (Johnson)			--xxxx---				---		x	x
43.	Limonia (M.) immatura (O. S.)				----						x
44.	Limonia (M.) triocellata (O. S.)				----xx-			---		x	x
45.	Limonia (Dis.) annulata (Linn.)					-				x	
46.	Limonia (D.) divisa Alex.			- ---xXx----x-----						x	x
47.	Limonia (D.) haeretica (O. S.)			--xx----						x	
48.	Limonia (D.) humidicola (O. S.)				-xx-					x	x
49.	Limonia (D.) immodestoides Alex.			----------				------		x	
50.	Limonia (D.) liberta (O. S.)			--xxXx----						x	x
51.	Limonia (D.) pudica (O. S.)			---xXx-						x	x
52.	Limonia (R.) bryanti (Johnson)				-						x
53.	Limonia (R.) domestica (O. S.)				------xxxXxx---			----x--		x	x
54.	Limonia (R.) lecontei Alex.			-							x
55.	Limonia (G.) communis (O. S.)			-xxXx---------				-		x	x
56.	Helius (H.) flavipes (Macquart)			---------				-		x	x
57.	Dicranoptycha elsa Alex.			-x-						x	x
58.	Dicranoptycha megaphallus Alex.			--xXx-						x	x
59.	Dicranoptycha pallida Alex.				------						x
60.	Dicranoptycha septemtrionis Alex.					--xx-------				x	
61.	Dicranoptycha sobrina O. S.				---					x	x
62.	Dicranoptycha tigrina Alex.						------			x	
63.	Epiphragma fasciapennis Alex.			--xXXxx---						x	x
64.	Epiphragma solatrix (O. S.)			--xx--		----------				x	x
65.	Pseudolimnophila contempta (O. S.)			---		----------				x	
66.	Pseudolimnophila luteipennis (O. S.)				--xx-		--------			x	x
67.	Pilaria imbecilla (O. S.)			--xx----							x
68.	Pilaria quadrata (O. S.)			--xXx------							x
69.	Pilaria tenuipes (Say)				-----xxxXXxx----					x	x
70.	Atarba (A.) picticornis O. S.				----xxx--					x	x

No.	Species	Mar. 1	2	3	Apr. 1	2	3	May 1	2	3	June 1	2	3	July 1	2	3	Aug. 1	2	3	Sept. 1	2	3	Oct. 1	2	3	Br.	NH.
71.	Elephantomyia (E.) westwoodi O. S.										-	-	-	-	-	-	-	-	-							x	x
72.	Cladura (C.) flavoferruginea O. S.																						-x	X	x-	x	x
73.	Chionea stoneana Alex.																									x	
74.	Teucholabis (T.) complexa O. S.										-																x
75.	Teucholabis (T.) lucida Alex.										-x	X	x-							-	-	-	-	-	-	x	x
76.	Gnophomyia tristissima O. S.							-	-	x	X	x	-	-	-	x	x	-	-	-	-	-	-	-	-	x	x
77.	Gonomyia (G.) florens Alex.											-															x
78.	Gonomyia (G.) kansensis Alex.										-																x
79.	Gonomyia (G.) subcinerea O. S.							-	-	x	X	x	x	-	-	-	-	-	-	-	-	-	x	-	-	x	x
80.	Gonomyia (L.) manca (O. S.)										-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	x	
81.	Gonomyia (L.) sulphurella O. S.																						-	-	-	x	
82.	Erioptera (S.) cana (Walker)	-	-	-	-	x	x	X	X	x	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	x	x
83.	Erioptera (E.) septemtrionis O. S.				-																					x	
84.	Erioptera (E.) vespertina O. S.							-	-	-	-															x	x
85.	Erioptera (M.) caliptera (Say)							-	-	x	X	x	-	-	-	-	x	x	-	-	-	-	-	-	-	x	x
86.	Erioptera (M.) needhami Alex.										-	-	-				-	-	-	-	-	-	-	-	-	x	
87.	Erioptera (M.) parva O. S.														-												x
88.	Erioptera (H.) armata O. S.				-	-	x	x	X	X	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x
89.	Erioptera (P.) graphica O. S.				-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				x
90.	Ormosia aenata (Doane)					-																				x	
91.	Ormosia ingloria Alex.																						-	-		x	
92.	Ormosia romanovichiana (O. S.)				-	x	-	-																		x	
93.	Tasiocera (D.) ursina (O. S.)							-	X	x	-															x	x
94.	Molophilus hirtipennis (O. S.)								-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		x
95.	Molophilus pubipennis (O. S.)								-	x	X	x	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x

Larvae were taken on April 3, 1974, from a thin carpet of moss covering a sodden, decayed log lying on the forest floor below the dam in NH.

Previously known range: Alberta to Nova Scotia, southward to Kansas and Florida.

4. *Nephrotoma alterna* (Walker)

Br. NH. 1974; June 5-July 16, with a single record for August 31; bivoltine.

Numerous in the bottomland woods, and in the moist thickets along streams; a few individuals from the low oak-hickory forests. On June 28, 1974, two females were found ovipositing into wet soil at the foot of a slope, about three feet from the margin of Coal Creek.

Previously known range: Michigan to Nova Scotia, southward to Florida.

5. *Nephrotoma eucera* (Loew)

NH. 1974; June 13.

Rare, one male taken from the tall,

luxuriant herbage around the swamp.

Previously known range: Wisconsin to Quebec and Massachusetts, southward to Kansas, Tennessee, and Virginia.

6. *Nephrotoma euceroides* Alexander

Br. NH. 1974-1975; May 23-June 26; univoltine.

Fairly common in grassy areas around the swamp, and in the bottomland woods where wood nettles and jewelweeds grow luxuriantly, less common in mesic hillside woods. When alarmed, flies up into the trees. This is the most common species of its genus found in the NH; larvae not found at Br. or NH. but were taken at Hole-in-the-Rock, 12 miles south of Lawrence, from soil next to a well-rotted stump.

Previously known range: Michigan to New Brunswick and Connecticut.

7. *Nephrotoma ferruginea* (Fabricius)

Br. NH. 1974-1975; April 21-June 29 and August 12-September 26; bivoltine (second generation records based on collections by G. W. Byers in 1969).

The first species of *Nephrotoma* to emerge in spring, and the only *Nephrotoma* found in grassland in the study areas. Numerous in the margins of the grassy fields and in adjacent woods. Rare in grassy patches along water courses. This species comes rather freely to light at night.

Previously known range: Eastern North America, westward to Colorado, southward to Texas.

8. *Nephrotoma macrocera* (Say)

Br. NH. 1974-1975; May 8-September 21. This species occurs throughout the summer with two peaks of emergence, in June and September; bivoltine.

This is the most abundant species of *Nephrotoma* in Br., fairly common in bottomland forests and more mesic parts of the oak-hickory; less common in the swampy area.

About a dozen, callow adults were taken on September 13, 1975, in grassy patches along Coal Creek, two days after a week-long rainy period.

Previously known range: Wisconsin to Maine, southward to Kansas, Tennessee, and Florida.

9. *Nephrotoma polymera* (Loew)

Br. NH. 1974-1975; May 22-June 28; univoltine.

Numerous to common in bottomland forests, and in grassy areas around the swamp. Rare in thickets along creeks.

Previously known range: Wisconsin to New Hampshire, southward to Kansas, Tennessee, and South Carolina.

10. *Nephrotoma virescens* (Loew)

Br. 1974-1975; June 11-July 23; univoltine.

Rare; only four specimens taken from wooded margins of Coal Creek, two of them, a mating pair, on June 11, 1974.

Previously known range: Michigan to New Hampshire, southward to Illinois and Florida.

11. *Tipula* (*Pterelachisus*) *ignobilis* (Loew)

NH. 1975; May 30-June 1; univoltine.

Rare and local, only seven specimens taken; three males from a small swarm at a small, vernal stream near the pond; two mating pairs from a moss-covered, tree trunk nearby on June 1, 1975. Adults were reared from larvae found in a mat of wet mosses on a cliff at Hole-in-the-Rock, 12 miles south of Lawrence.

Previously known range: Illinois to New Brunswick, southward to Tennessee and North Carolina.

12. *Tipula* (*Pterelachisus*) *trivittata* Say

Br. NH. 1975; May 3-19; univoltine.

Rare; from the bottomland forests, or from moist to mesic hillside woods. The Malaise trap in the Br. caught four individuals of this species.

Previously known range: Iowa to Newfoundland, southward to Tennessee and South Carolina.

13. *Tipula* (*Lunatipula*) *australis* Doane

NH. May 1958 and May 1960; univoltine.

Records based on collections made by G. W. Byers. A spring species, found in 1958 on the shaded bank of the overflow channel around the dam (NH). In 1960, recorded from the brushy hillside just below an old limestone quarry in the NH.

Previously known range: Texas to Georgia, northward to Maryland.

14. *Tipula* (*Lunatipula*) *bicornis* Forbes

Br. NH. 1974-1975; May 7-June 4; univoltine.

Abundant and local in grassland, rare or absent elsewhere; adults usually on pink clover or other, taller, herbaceous plants in grassy fields. On the morning of May 8, 1975, about 20 pairs were observed in copulation, one foot or less above the ground in a grassy field along the highway at the edge of the Br. In every instance the male was fully matured, the female slightly or very teneral.

Pupae were taken on May 4, 1975, in grassland, about 6 mm. beneath the ground surface, which was covered by a thin mat of mosses. Adults emerged on 10 May; several of these and some of the pupae were killed by fungus, *Massospora tipulae* Porter (identified by Dr. R. W. Lichwardt of the University of Kansas Department of Botany).

Previously known range: Wisconsin to New Brunswick, southward to Kansas, Tennessee, and Virginia.

15. *Tipula* (*Lunatipula*) *dietziana* Alexander

Br. NH. 1975; April 28-May 6; univoltine.

Numerous and general on moist, north-facing hillsides. In morning and late afternoon many males were seen flying about over the damp leaf mold well up the slopes of the hillside woods, probably in search of emerging females.

Previously known range: Kansas to New York, and South Carolina.

16. *Tipula* (*Lunatipula*) *disjuncta* Walker

NH. 1975; April 29-May 7; univoltine.

Numerous and general in oak-hickory forests, rare on lower mesic hillsides. Males are very active during the day, searching for emerging females. All specimens taken were males; females recorded from G. W. Byers' collection of May 10, 1960.

Previously known range: Iowa to Vermont, southward to Illinois and Delaware.

17. *Tipula* (*Lunatipula*) *dorsimacula* Walker

Br. NH. 1975; April 20-May 4; univoltine.

The earliest of the subgenus *Lunatipula* to emerge in the spring; numerous on mesic hillsides and in vernal seepage areas. In the morning, males were usually found flying low over the damp leaf mold, together with males of *T. dietziana*.

Previously known range: British Columbia to Nova Scotia, southward to California and New Jersey.

18. *Tipula* (*Lunatipula*) *duplex* Walker

Br. NH. 1974-1975; May 27-July 26; univoltine, with a long adult flight period, at its peak in mid-June. Females rare after mid-July. The long season is probably correlated with local differences in habitats.

Abundant in oak-hickory and hillside

woods, common in bottomland forests, and rare in the swamp area, this is the most abundant and conspicuous *Tipula* of mid-June. Adults range throughout wooded habitats.

Previously known range: Kansas to Nova Scotia and Florida.

19. *Tipula* (*Lunatipula*) *flavibasis* Alexander

Br. NH. 1974-1975; June 19-July 24; univoltine.

The last species of *Lunatipula* to emerge in summer; numerous in margins of rather dry woodlands, spreading into adjacent, grassy fields.

Previously known range: Kansas.

20. *Tipula* (*Lunatipula*) *flavoumbrosa* Alexander

Br. NH. 1974-1975; May 8-June 10; univoltine.

Abundant in the low, damp parts of the oak-hickory and bottomland forests, rare from drier and open parts of hillside woods. Most often found on upper leaves of low shrubs.

Previously known range: Kansas to Michigan, South Carolina, and Florida.

21. *Tipula* (*Lunatipula*) *fuliginosa* (Say)

Br. NH. 1974-1975; May 17-June 10; univoltine.

Numerous in drier parts of hillside woods, a few in the oak-hickory woods. Females usually in damp thickets along the creek and moist, grassy patches in bottomland woods.

Previously known range: Kansas to Ontario and New Hampshire, southward to North Carolina.

22. *Tipula* (*Lunatipula*) *mallochi* Alexander

Br. NH. 1974-1975; May 12-June 17; univoltine.

Abundant in moist, low oak-hickory, in bottomland forests and damp thickets along the creeks, common in wooded margins of the swamp, widespread in woods in late May. Larvae were taken at Hole-in-the-Rock beneath and in leaf mold of the forest floor. These began to pupate April 26, 1974, and adults started emerging on May 3.

Previously known range: Missouri to Maryland and Florida.

23. *Tipula* (*Lunatipula*) *morrisoni* Alexander

Br. NH. 1974-1975; May 23-June 17, univoltine.

Numerous in open woods and drier hillside woods; adults usually among lower leaves of trees.

Previously known range: Kansas to Rhode Island, southward to Mississippi, and South Carolina.

24. *Tipula* (*Lunatipula*) *perlongipes* Johnson

Br. NH. 1974-1975; May 30-June 20; univoltine.

Rare, on drier, sparsely wooded, oak-hickory slopes; distinguished from other members of the *triplex* subgroup by the relatively narrow, yellow wings, and by male genitalial structures.

Previously known range: Florida, North Carolina to Indiana.

25. *Tipula* (*Lunatipula*) *triplex* group, species near *T. perlongipes*

Br. 1975; May 31-June 17; univoltine.

Rare in bottomland woods and more mesic parts of the low oak-hickory. It differs from *perlongipes* in the structure of the male hypopygium, which lacks the median depressed lobe on the 8th sternum (Fig. 29). The habitat distribution of this species is more like that of *T. flavoumbrosa*. Rogers (1942) called this species *Tipula* species, *triplex* group near *flavoumbrosa*.

Previously known range: Michigan, westward to Iowa, and Missouri (Rogers, 1942, p. 68).

26. *Tipula* (*Lunatipula*) *translucida* Doane

NH. 1974-1975; June 10-June 17; univoltine.

Rare and local in a narrow thicket along the overflow channel at the pond in the NH. All specimens caught were males, usually among leaves of taller buckbrush and lower branches of trees.

Previously known range: Illinois to Pennsylvania, southward to Oklahoma and South Carolina.

27. *Tipula* (*Lunatipula*) *triplex* Walker

Br. NH. 1974-1975; May 7-May 31; univoltine.

Common in the ecotone between grassy fields and edges of woods. Several teneral adults were taken from the grassy field along with *T. bicornis* on May 8, 1975. Rare or absent in other habitats.

Previously known range: Alberta to Newfoundland, southward to Wisconsin and Virginia.

28. *Tipula* (*Lunatipula*) *integra* Alexander

Br. NH. 1974-1975; May 8-June 6; univoltine.

Common in the wetter, low, oak-hickory and hillside woods, absent in grassland, rare in bottomland forests. Resembles *T. triplex,* from which it differs in details of male genitalia. The submedian teeth of the 8th sternum are broad at base with round apex in this species (Fig. 26). It also appears to have a somewhat different habitat.

Rogers (1942) believed this form is distinct from either *triplex* or *umbrosa* and used the term *Tipula triplex* group form C for it. Alexander (1962) described it as *Tipula triplex integra,* a race of *triplex.* However, the conspicuous differences in male genitalial structure, habitat correlation, and occurrence together with the typical form suggest it is a distinct species.

Previously known range: Michigan, Indiana.

29. *Tipula* (*Lunatipula*) *tuscarora* Alexander

Br. 1974-1975; May 17-June 2; univoltine.

Rare in open woodland; easily flushed and usually alights on lower leaves of trees. All specimens taken were males.

Previously known range: Missouri to Maryland, southward to South Carolina.

30. *Tipula* (*Platytipula*) *paterifera* Alexander

Br. NH. 1974-1975; October 10-21; univoltine.

One female was taken in a grassy patch along Coal Creek in 1974. In 1975 this species was found abundant in the patches of *Polygonum* which conceal the pond shoreline at NH. It was also common in the grassland where *T. bicornis* was found in the spring. Adults are active in late afternoon. This species comes frequently to light at the home of the resident naturalist at NH.

Previously known range: Tennessee, Missouri.

31. *Tipula* (*Platytipula*) *ultima* Alexander

Br. NH. 1974-1975; August 29-October 10; univoltine.

Abundant in the transition zones between the swamp and mesic hillside woods, this species also spreads into adjacent grasslands. About 60 larvae were taken on April 3, 1974, in saturated soil on the bank of the overflow channel around the dam at NH. These were reared and observed in the laboratory. They stopped feeding and moved from the saturated soil to drier soil in early July, although pupation did

not occur until about a week before emergence, which started on September 3, 1974.

Previously known range: Saskatchewan to Nova Scotia, southward to Wyoming, Mississippi, and Florida.

32. *Tipula* (*Trichotipula*) *unimaculata* (Loew)

Br. NH. 1974-1975; June 24-July 16; univoltine.

Rare in wet areas in hillside woods. Often found resting on algae-covered tree trunks near hillside seepage areas.

Previously known range: Michigan to Maine, southward to Illinois, and North Carolina.

33. *Tipula* (*Trichotipula*) *stonei* Alexander

Br. 1974-1975; September 5-21; univoltine.

Occasionally numerous on open hillsides; adults found resting on leaves of lower branches of trees.

Previously known range: Michigan to Ontario, southward to Kansas and Florida.

34. *Tipula* (*Yamatotipula*) *furca* Walker

Br. NH. 1974-1975; April 21-June 29, and August 31-September 8; bivoltine.

Common in the swamp area at NH. and in grassy patches along Coal Creek; rare in damp thickets around the swamp.

Females were observed ovipositing into saturated soil at the margin of the pond and along the bank of a brook which feeds into the pond at NH.

Previously known range: Kansas to Quebec and Maine, southward to Texas and Florida.

35. *Tipula* (*Yamatotipula*) *sayi* Alexander

Br. 1974-1975; September 13-14; univoltine.

Only two females taken, both from a grassy clearing in the flood-plain woods along Coal Creek.

Previously known range: Iowa to Newfoundland, southward to Louisiana and Florida, Bermuda.

36. *Tipula* (*Yamatotipula*) *strepens* Loew

Br. NH. 1974-1975; May 1-June 26, and July 24-August 17; bivoltine.

Common in grassy areas around the swamp and in grassy patches along Coal Creek. Numerous in the damp thicket around the swamp, usually found hanging in buck brush.

T. strepens and *T. furca* overlap to some extent in their habitat; *strepens* apparently is able to tolerate lower humidity than *furca*.

Previously known range: Kansas to Newfoundland, southward to New Jersey.

37. *Tipula* (*Yamatotipula*) *tricolor* Fabricius

NH. 1975; May 23-June 1; apparently univoltine here, though bivoltine elsewhere in eastern U.S.

Rare and local in the swamp area; all three specimens were taken from patches of *Polygonum hydropiper* growing at the edge of the pond.

Previously known range: Wisconsin to Quebec and Maine, southward to Arkansas and Florida.

38. *Limonia* (*Limonia*) *globithorax* (Osten Sacken)

Br. 1974; August 17-September 18; univoltine.

Numerous and local; six specimens were taken from a small swarm above a partially submerged, fallen, tree trunk in Coal Creek. Three records were from damp, decayed wood in a nettle patch along the creek.

Previously known range: Wisconsin to Newfoundland, southward to Tennessee and Florida.

39. *Limonia* (*Limonia*) *rara* (Osten Sacken)

Br. NH. 1974-1975; June 14-July 23, and August 17-September 18; bivoltine.

Numerous and general in its restricted habitats along water courses. Most specimens were resting on moist, moss-covered tree trunks about 18 inches above the ground, in mesic flood plain forest.

Previously known range: Iowa and Wisconsin to New York, southward to Florida.

40. *Limonia* (*Limonia*) *tristigma* (Osten Sacken)

Br. NH. 1974-1975; June 10-July 3; univoltine.

The most abundant species of subgenus *Limonia* in two study areas. Abundant in the flood plain forests and swamp, especially in places where nettle and jewelweed are luxuriant, occasionally hanging from stems and leaf margins of tall herbs and shrubs.

Previously known range: Alberta to New Brunswick, southward to Tennessee and North Carolina.

41. *Limonia* (*Metalimnobia*) *cinctipes* (Say)

Br. NH. 1974; June 11-25; univoltine.

Rare, in mesic, low oak-hickory and the thickets between hillside woods and swamp. A female was found resting on the shady side of a tree trunk with wings folded over the back and all legs outspread.

Previously known range: Alberta to Newfoundland, southward to Mississippi and Florida.

42. *Limonia* (*Metalimnobia*) *fallax* (Johnson)

Br. NH. 1974-1975; May 3-June 25, and September 5-14; bivoltine.

Numerous in the low, oak-hickory forests, adults usually standing on leaf litter around seepage or wet spots, or on moist, decayed tree stumps.

Previously known range: Michigan to New Jersey, southward to Oklahoma and North Carolina.

43. *Limonia* (*Metalimnobia*) *immatura* (Osten Sacken)

NH. 1974-1975; June 19-July 2; univoltine.

Rare, in mesic hillside thickets. Two of the three specimens were from the same habitat as *L. cinctipes,* the other one from jewelweeds in bottomland woods.

Previously known range: Maine to British Columbia, southward to Florida.

44. *Limonia* (*Metalimnobia*) *triocellata* (Osten Sacken)

Br. NH. 1974-1975; May 24-June 26, and September 5-14; bivoltine.

Numerous in upland woods, where the scattered undergrowth is about two feet high. Adults often rest on shrubs. Apparently this species can tolerate low humidity better than other members of its genus.

Previously known range: Alberta to Nova Scotia, southward to Tennessee and Georgia.

45. *Limonia* (*Discobola*) *annulata* (Linnaeus)

Br. 1975; July 16.

Rare and local, only two males having been taken from dry moss-covered bases of trees in bottomland woods bordering Coal Creek.

Previously known range: British Columbia to Newfoundland, southward to Oregon, Tennessee, and Virginia; also found in Eurasia, south to New Guinea.

46. *Limonia* (*Dicranomyia*) *divisa* Alexander

Br. NH. 1974-1975; April 21-July 16. Continuous flight period, but a definite

peak of abundance in late May; probably bivoltine.

Numerous to common in bottomland woods and mesic parts of oak-hickory woods, especially in shaded ravines having moist to wet banks. Females were observed ovipositing in moist moss on fallen trees.

Previously known range: Iowa to Massachusetts, southward to Missouri and Florida and the Greater Antilles.

47. *Limonia* (*Dicranomyia*) *haeretica* (Osten Sacken)

Br. 1974-1975; May 3-June 10; univoltine.

Numerous in vernal, seepage areas; most specimens taken in 1975 were under a moss-covered, overhanging rock on a shaded, wet hillside. Rare or absent in all other, drier habitats. Adults were reared from larvae from mosses growing on cliff at Hole-in-the-Rock, 12 miles south of Lawrence.

Previously known range: Newfoundland and Rhode Island, westward to Michigan.

48. *Limonia* (*Dicranomyia*) *humidicola* (Osten Sacken)

Br. NH. 1974; June 11-28; univoltine.

A typical stream species, generally distributed in wet, well-shaded spots along streams and in the wet, wooded ravine; usually found in shaded niches where *Dolichopeza* was common.

Previously known range: British Columbia to Nova Scotia, southward to California, Central America and northern Georgia.

49. *Limonia* (*Dicranomyia*) *immodestoides* Alexander

Br. 1974-1975; May 6-June 25, and August 31-September 12; bivoltine.

Rare and local; the few records were from hillside woods with luxuriant undergrowth. Absent from better drained woodlands.

Previously known range: Oregon to Newfoundland, southward to Indiana.

50. *Limonia* (*Dicranomyia*) *liberta* (Osten Sacken)

Br. NH. 1974-1975; May 1-June 20; univoltine.

Common in vernal seepage in bottomland woods and in the mesic thicket around the margin of the pond in the NH. Rare to absent on the slopes.

Previously known range: Manitoba to Newfoundland, southward to Oklahoma and Florida, and in Bermuda.

51. *Limonia* (*Dicranomyia*) *pudica* (Osten Sacken)

Br. NH. 1974-1975; April 29-May 31; univoltine.

Common in spring, generally distributed in bottomland woods where the understory is luxuriant, less common in poorly drained woodland.

Previously known range: Michigan to Maine, southward to Illinois and North Carolina.

52. *Limonia* (*Rhipidia*) *bryanti* (Johnson)

NH. 1974; June 17.

Rare, only one male taken beneath a protruding rock by one of the brooks which feed into the pond.

Previously known range: Colorado to Maine, southward to Arizona and Florida.

53. *Limonia* (*Rhipidia*) *domestica* (Osten Sacken)

Br. NH. 1974-1975; May 8-July 16 and September 5-October 10; bivoltine.

Abundant and generally distributed in moist creek-margin thickets, beneath shaded banks of ravines, in flood plain woods and near seepages and the swamp; a few spread into drier, upland woods.

Previously known range: Kansas and

Iowa to New Jersey, southward to Texas and Florida; also in the neotropical region.

54. *Limonia* (*Rhipidia*) *lecontei* Alexander

NH. 1974; May 19.

One male taken from a decayed, partially submerged log in the brook just below the dam in the NH.

Previously known range: Alaska to Newfoundland, southward to California, and Virginia; also recorded from Eurasia.

55. *Limonia* (*Geranomyia*) *communis* (Osten Sacken)

Br. NH. 1974-1975; April 16-June 26 and September 20; bivoltine.

Common and local in the continuously-wet to slightly-submerged layer of algae in the stream bed and the submerged film of algae on the margin of the stream where the water is quiet. Adults of both sexes occurred along the brook, and females were observed ovipositing on algae-covered rocks in the brook at NH.

Previously known range: Ontario westward to Washington and Califonia, southward to Florida. This species has frequently been confused with *L.* (*G.*) *canadensis* in the literature, as noted by Alexander (1965:49).

56. *Helius* (*Helius*) *flavipes* (Macquart)

Br. NH. 1974-1975; May 8-July 16 with a single record for September 14; bivoltine.

Rare, only six specimens, from near the swamp and from bottomland woods. Adults usually rest on tall herbs.

Previously known range: Alberta to Nova Scotia, southward to Texas and Florida.

57. *Dicranoptycha elsa* Alexander

Br. NH. 1974-1975; May 22-June 3; univoltine.

Numerous in the same situations where *D. megaphallus* was found. Adults were mostly from shrubs such as buckbrush, less commonly from poison ivy and other herbs.

Previously known range: New York to North Carolina.

58. *Dicranoptycha megaphallus* Alexander

Br. NH. 1974-1975; May 23-June 17; univoltine.

This is the most common species of its genus in the two study areas; characteristic of oak-hickory and spreading into nearby habitats. As in all species of the genus, the adults at rest stand upright, high on the tarsi, with body elevated above the upper surfaces of leaves, with the wings folded over the back.

Previously known range: North Carolina, South Carolina, and Florida.

59. *Dicranoptycha pallida* Alexander

NH. 1974-1975; June 24-July 16; univoltine.

Rare and apparently very local; all records are from swamp and low oak-hickory ecotones, where dense thickets are formed, with rich undergrowth.

Previously known range: Kansas, Indiana.

60. *Dicranoptycha septemtrionis* Alexander

Br. 1974-1975; July 16-September 7; univoltine.

Numerous in flood plain woods, from patches of nettles and jewelweed, less common in open woods on hillside slopes.

Previously known range: Michigan to Massachusetts, southward to Indiana and North Carolina.

61. *Dicranoptycha sobrina* Osten Sacken

Br. NH. 1974-1975; June 10-17; univoltine.

Rare; three specimens were swept from a rather dry, open, hillside woods, where the undergrowth was largely tick trefoil (*Desmodium*).

Previously known range: Indiana to

New Jersey, southward to Tennessee and Florida.

62. *Dicranoptycha tigrina* Alexander

Br. 1974; August 31-September 21; univoltine.

Rare; and rather local, all records being from grassy patches along Coal Creek, the flies usually found in the places where *D. septemtrionis* is common.

Previously known range: Indiana, Illinois, Tennessee, and North Carolina.

63. *Epiphragma fasciapennis* (Say)

Br. NH. 1974-1975; May 12-June 28; univoltine.

Common in the latter half of May and early June, and rather generally distributed in bottomland woods, in the swamp, and in dense thickets between the swamp and low oak-hickory; adults usually found on forest litter or low shrubs, less than two feet above ground.

Previously known range: Alberta to Newfoundland, southward to Louisiana and Florida.

64. *Epiphragma solatrix* (Osten Sacken)

Br. NH. 1974-1975; May 14-June 10 and July 15-September 14; bivoltine.

Common in the margins of the swamp and in bottomland forests, spreading into moist thickets nearby. Larvae were taken in April, 1974, from both wet, submerged wood in a brook and a decayed log on the forest floor. Adults emerged on May 2, 1974.

Flies of the summer generation have a smaller body size than those of the spring generation.

Previously known range: Missouri to New York, southward to Louisiana and Florida.

65. *Pseudolimnophila contempta* (Osten Sacken)

Br. 1974-1975; May 24-June 3, and August 3-September 21; bivoltine.

Rare, all specimens from the vicinity of shaded, hillside seepage areas. Adults were found resting on the ground rather than on plants.

Previously known range: Michigan to Newfoundland, southward to Missouri and Florida.

66. *Pseudolimnophila luteipennis* (Osten Sacken)

Br. NH. 1971-1975; June 1-25, and August 17-September 21; bivoltine.

Numerous in the grassy edges of the swamp at NH. and in grassy patches along Coal Creek, spreading onto lower, more densely shaded hillsides. Adults were found on the wet ground rather than on plants.

Previously known range: Quebec westward to California and southward to Louisiana and Florida.

67. *Pilaria imbecilla* (Osten Sacken)

NH. 1974-1975; May 15-June 19; univoltine.

Locally common at margins of the pond, rarely spreading into nearby thickets. Adults usually rest on leaves of shrubs and taller herbage.

Previously known range: Illinois to Quebec and Massachusetts, southward to Tennessee and Georgia.

68. *Pilaria quadrata* (Osten Sacken)

NH. 1974-1975; April 29-June 19; univoltine.

Fairly common, but local, in the vicinity of the pond; adults found in great numbers on May 3, 1975, on the muddy edges of the pond, on *Polygonum hydropiper* that grows around the pond, less common in the wet thickets nearby.

Previously known range: Iowa to Nova Scotia, southward to Florida.

69. *Pilaria tenuipes* (Say)

Br. NH. 1974-1975; May 3-July 16; univoltine.

The most common species of its genus; common and generally distributed in wet thickets around the swamp and along creeks, also common in the flood plain forests, rare in mesic hillside woods. Adults were found usually standing on leaves of taller shrubs, with wings folded over the back and an elevated stance resembling that of *Dicranoptycha*.

In localities where all three species of *Pilaria* were found, *quadrata* occurred in the wettest microhabitats, *tenuipes* in the less mesic habitat, while *imbecilla* was found in between.

Previously known range: Wisconsin to New Brunswick, southward to Kansas, Texas, and Florida.

70. *Atarba* (*Atarba*) *picticornis* Osten Sacken

Br. NH. 1974-1975; May 22-July 2, and a single record on September 21; bivoltine.

Numerous in grassy areas along the overflow channel around the dam in NH., in nettle-jewelweed patches along Coal Creek, and rare in mesic thickets and hillside habitats.

Previously known range: Michigan to New Hampshire, southward to Missouri and Florida.

71. *Elephantomyia* (*Elephantomyia*) *westwoodi* Osten Sacken

Br. NH. 1974-1975; June 2-July 23; univoltine.

Rare, only five specimens taken, all from low, oak-hickory slopes. Adults were found hanging from leaves on low branches of trees.

Previously known range: Wisconsin to Newfoundland, southward to Illinois and Florida.

72. *Cladura* (*Cladura*) *flavoferruginea* Osten Sacken

Br. NH. 1974-1975; October 2-21; univoltine.

This species emerges in the dry autumn and is the last tipulid species that occurs in these areas, except for the winter species *Chionea stoneana*. Adults common and generally distributed in most of the woods.

Previously known range: Wisconsin to Quebec and Maine, southward to Missouri and Georgia.

73. *Chionea stoneana* Alexander

Br. 1973; January 20. The only nearly apterous crane fly in the local fauna; univoltine.

G. W. Byers collected one live male in a pitfall trap, set by an old rubbish dump that had numerous mouse burrows beneath slabs of wood, etc. At other places, he has found *C. stoneana* in burrows and nests of mice.

Previously known range: Illinois.

74. *Teucholabis* (*Teucholabis*) *complexa* Osten Sacken

NH. 1974; June 5.

Two specimens taken from near a vernal, seepage area, both resting on leaf litter.

Previously known range: Michigan to Connecticut, southward to Oklahoma and Florida.

75. *Teucholabis* (*Teucholabis*) *lucida* Alexander

Br. NH. 1974-1975; May 31-June 17 and August 17-October 2; bivoltine.

Common and local in swampwoods in early summer when the water level of the pond began to drop and small bodies of water were ponded by tree roots and forest litter. Adults were resting on saturated soil around this water. Also recorded from the shaded bank of the ravine at Br.

Previously known range: Missouri to

District of Columbia, southward to Florida.

76. *Gnophomyia tristissima* Osten Sacken

Br. NH. 1974-1975; May 7-July 16; univoltine.

Common in bottomland woods and wet thickets on herbage among fallen, decaying trees.

Previously known range: Northwest Territories to Quebec and Maine, southward to Texas and Florida.

77. *Gonomyia* (*Gonomyia*) *florens* Alexander

NH. 1974; June 24.

One male only, from the grassy margin of a brook at NH.

Previously known range: Michigan to Quebec and Maine, southward to Illinois, Tennessee, and North Carolina.

78. *Gonomyia* (*Gonomyia*) *kansensis* Alexander

NH. 1956; May 28.

This record based on a light trap collection made by G. W. Byers in 1956.

Previously known range: Oklahoma, Missouri, Illinois, Indiana, and Michigan.

79. *Gonomyia* (*Gonomyia*) *subcinerea* Osten Sacken

Br. NH. 1974-1975; May 8-June 16 and August 3-October 10; bivoltine.

This is the most abundant species of its genus; common and generally distributed in oak-hickory and mesic bottomland woods.

Previously known range: British Columbia to Newfoundland, southward to Utah, Kansas, and Florida.

80. *Gonomyia* (*Lipophleps*) *manca* (Osten Sacken)

Br. 1974-1975; June 2-August 17; univoltine.

Rare, a total of twelve specimens taken in bottomland woods, mainly from grassy margins of Coal Creek.

Previously known range: Indiana to Massachusetts, southward to Tennessee, and Florida.

81. *Gonomyia* (*Lipohphleps*) *sulphurella* Osten Sacken

Br. 1974-1975; September 5-13; univoltine.

Rare, only two males taken from the same wooded ravine at Br.

Previously known range: Kansas to Newfoundland, southward to Texas and Florida.

82. *Erioptera* (*Symplecta*) *cana* (Walker)

Br. NH. 1974-1975; March 21-May 30 and September 21-29; multivoltine.

The first species to appear in the spring, when most vegetation has not yet started growing; abundant in the spring in nearly all wooded habitats and open grasslands. The fall generation was inconspicuous.

Previously known range: Alaska, throughout southern Canada and the United States.

83. *Erioptera* (*Erioptera*) *septemtrionis* Osten Sacken

Br. 1975; April 17.

One female from a juniper tree growing at the ecotone between woods and grassy field.

Previously known range: Washington to Newfoundland, southward to California, Kansas, and Florida.

84. *Erioptera* (*Erioptera*) *vespertina* Osten Sacken

Br. NH. 1975; May 7-22; univoltine.

Numerous; all but two were from the Malaise traps, those two swept from grassy patches near the traps.

Previously known range: Iowa to Nova Scotia, southward to Alabama and Florida.

85. *Erioptera* (*Mesocyphona*) *caliptera* (Say)

Br. NH. 1974-1975; May 7-June 24 and July 16-August 21; bivoltine.

Abundant where soil is wet or muddy during most of the year, in bottomland forests, swampwoods, and grassy margins of streams; not spreading into the drier oak-hickory woods, but may spread to mesic hillside woods.

Previously known range: California to Newfoundland, southward to Florida; also Neotropical.

86. *Erioptera* (*Mesocyphona*) *needhami* Alexander

Br. 1974-1975; May 31-June 11 and August 3-17; bivoltine.

Rare, only four specimens swept from grassy areas along the sandy creek shore, and two from a shaded bank of Coal Creek.

Previously known range: Missouri to Nova Scotia, southward to Florida.

87. *Erioptera* (*Mesocyphona*) *parva* Osten Sacken

NH. 1975; July 24.

One male specimen taken from a grassy area in the swamp woods.

Previously known range: Kansas to Michigan and Connecticut, southward to Florida.

88. *Erioptera* (*Hoplolabis*) *armata* Osten Sacken

Br. NH. 1974-1975; April 19-June 14 and July 25-August 17; bivoltine.

Abundant; adults taken along all water courses, either from shaded banks or from the base and roots of large trees growing by creeks. Large swarms seen on April 28, 1975, along Coal Creek, about five feet above ground.

Conspicuous, bimodal variation was found in the dististyles of local males, suggesting that two species might have been represented.

Previously known range: Colorado to Newfoundland, southward to Oklahoma and Georgia.

89. *Erioptera* (*Psiloconopa*) *graphica* Osten Sacken

NH. 1974-1975; April 22-June 26 and September 29; bivoltine.

Numerous and local about the margins of the pond, less numerous in the swamp woods and rare elsewhere, all individuals on herbaceous plants.

Previously known range: Nebraska to Ontario and Massachusetts, southward to Louisiana and Florida.

90. *Ormosia arcuata* (Doane)

Br. 1975; April 28.

One female recorded from the grassy margin of Coal Creek.

Previously known range: Alberta to New Brunswick, southward to Tennessee.

91. *Ormosia ingloria* Alexander

Br. 1975; September 7-13; univoltine.

Rare; all specimens collected were males, most found resting on tree trunks growing in bottomland and on hillsides. One was taken from a tall shrub.

Previously known range: Indiana and Ontario.

92. *Ormosia romanovichiana* (Osten Sacken)

Br. 1975; April 19-28; univoltine, in early spring.

Common in spring along the creek and around most vernal seepages, usually resting on wet, moss-covered rocks or on tree bark, where *Erioptera* (*H.*) *armata* was also common. These two species can be easily differentiated in the field by the way they rest on the substrate. This species holds its body parallel to the substrate, while *E. armata* always tilts its body, head

downward, to form an angle with the substrate.

Previously known range: Illinois to Maine, southward to Tennessee and South Carolina.

93. *Tasiocera* (*Dasymolophilus*) *ursina* (Osten Sacken)

Br. NH. 1975; May 6-14; univoltine.

Locally abundant near seepage areas and shaded brooks. On May 7 at 10 a.m. I took about forty males from swarms about two feet above ground along brooks leading to the pond at the NH. One mating pair was found at that time. All other females were from the Malaise trap at the NH.

Previously known range: Newfoundland, southward to Tennessee and North Carolina.

94. *Molophilus hirtipennis* (Osten Sacken)

NH. 1974-1975; May 15-June 13; univoltine.

Rare; only three females were taken from grassy patches in the swamp woods.

Previously known range: Ontario to Newfoundland, southward to Illinois, Tennessee, and North Carolina.

95. *Molophilus pubipennis* (Osten Sacken)

Br. NH. 1974-1975; May 6-June 11; univoltine.

Common to abundant in damp to wet, flood plain forests, and on damp, coarse, sand bars in the bed of Coal Creek. All specimens were females. Rogers (1942) believed that this species as well as *M. hirtipennis* is chiefly or entirely parthenogenetic.

Previously known range: Michigan to Quebec and Newfoundland, southward to Florida.

DISCUSSION

Crane flies occupy many types of habitats in their immature and adult stages. The larval habitat of most species is local and restricted. Certain species live in mud, some in decaying, vegetable detritus, while others occur in rotting wood. Many larvae are scavengers, others are herbivores and still others are predaceous. In most cases, the presence or absence of a suitable, larval habitat determines whether a species can maintain itself in a given area.

During this two-year investigation, 95 species of crane flies were recorded from the two study areas, of which 56 species were common to both areas. Another 21 species were found only at the Breidenthal Reserve, the remaining 18 species only at the Natural History Reservation. Other species and subspecies recorded from northeastern Kansas, but not taken in either of the study areas are: *Dolichopeza* (*Oropeza*) *polita pratti, Tipula* (*Schummelia*) *hermannia, T.* (*Nippotipula*) *abdominalis, T.* (*Beringotipula*) *borealis, T.* (*Lunatipula*) *incisa kansensis, Limonia* (*Geranomyia*) *rostrata, Dicranoptycha minima, Erioptera* (*Psiloconopa*) *armillaris,* and *E.* (*P.*) *venusta.*

The crane-fly fauna of eastern Kansas is relatively poor when contrasted with the faunas of the eastern states: New England (Johnson, 1925, and Alexander, 1925, 1927, 1930, 1936) has 337 species; New York (Alexander, 1919, 1922, 1924, 1929), 318 species; southeastern Michigan (Rogers, 1942), 201 species. This can be explained largely by the geographical location of Kansas. Eastern Kansas is located in a transition zone between the eastern forests and the central plains. The prairie forms a natural barrier, preventing the eastward spread of western species. Consequently, there is an abrupt difference in crane fly fauna between eastern Kansas and mountainous central Colorado. Most Kansas crane flies are eastern species, occurring also in forests and other appropriate habitats eastward to the Atlantic Ocean. Since crane flies are more abun-

dant in moist woodlands, the relatively small number of tipulid species in eastern Kansas is probably due to the decline of forests from east to west.

Climate also affects the distribution of crane flies. The subfamily Limoniinae is more abundantly represented in the humid eastern forests and decreases westward, as average humidity gradually drops. In terms of percentage of the total crane fly fauna, the situation is reversed for the subfamily Tipulinae. This can be seen by comparing the percentage of Tipulinae in New England—34% of 337 species (Johnson, 1925, Alexander, 1925, 1927, 1930, 1936), in New York—29% of 318 (Alexander, 1919, 1922, 1924, 1929), in Tennessee —30% of 151 (Rogers, 1930), in Ohio— 34% of 146 (Foote, 1956), in Michigan— 36% of 201 (Rogers, 1942), and in eastern Kansas—39% of 95. The significance of the increasing percentage of Tipulinae can be shown by use of the chi-square test (Snedecor, 1956). It is noteworthy that no species of the large genus *Limnophila* have been found in eastern Kansas. *Limnophila* comprises 14% of the crane fly fauna in New England, 17% in New York, 9% in Tennessee, 8% in Ohio, 9% in Michigan. Most other aquatic, predaceous genera such as *Hexatoma* and *Pedicia* are also absent from Kansas. The absence in Kansas of marshes, bogs, and other permanently wet habitats, other than artificial ponds (all of relatively recent origin) and a few major streams, usually very muddy, probably accounts for the absence of these genera.

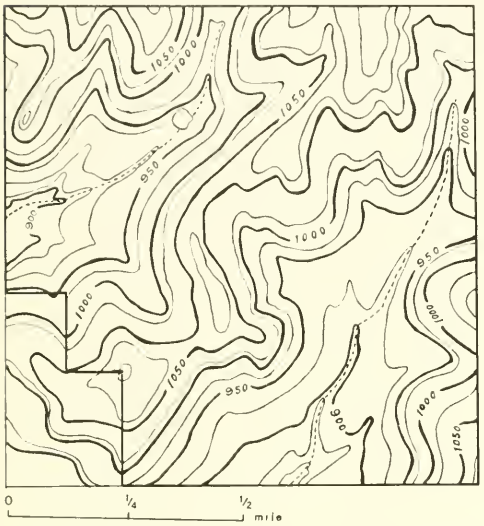
The differences in distribution of species in the two study areas are due more to topographic than to climatic conditions, since there is no significant difference in climatic conditions between the two areas. The general floras of the two areas are obviously quite different, although there are many species common to both. Since the Natural History Reservation was not established until thirty years ago, its vegetation is still in a successional state, in which climax oaks and hickories do not yet dominate much of the area. In the Breidenthal Reserve, the vegetation has reached a stable, climax state.

The two areas differ in humidity and water drainage. Within the Breidenthal Reserve, Coal Creek is a well-developed stream, supplied by numerous, short tributaries, so that it flows during most of the year. The slopes around the creek are relatively steep. The hillsides immediately bordering the creek rise 200 feet in less than a quarter of a mile. Apparently much of the rain that falls on the high land surrounding the Coal Creek ravine at first becomes groundwater, but later seeps through the steep hillsides to feed moisture into the ravine. Three additional factors contribute to retention of moisture in the Coal Creek ravine. A large proportion of the vegetation at the Breidenthal Reserve has reached the climax stage and retains moisture well. The ravine opens toward the northeast and its outlet is greatly restricted by ridges which make it an enclosed basin, as a result of which it is protected from the southwestern summer winds of eastern Kansas. Finally, there are many relatively steep, north-facing slopes at the Breidenthal Reserve, resulting in shade and, consequently, less evaporation. The total result is higher humidity at the Breidenthal Reserve than at the Natural History Reservation.

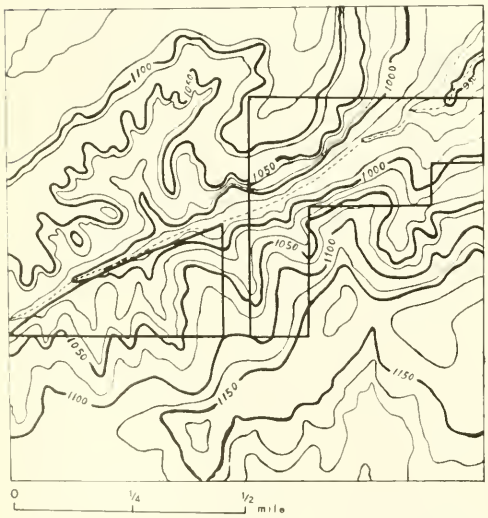
On the Natural History Reservation the streams are small and intermittent, being near their headwaters. They dry out shortly after the beginning of summer. While the total relief is comparable to that of the Breidenthal Reserve, the slopes are generally not as steep, and many of the streams follow ravines which open directly to the southwest and so are exposed to the drying effects of summer winds. Furthermore, much of the vegetation at the Nat-

ural History Reservation is still successional and holds less moisture.

The investigation made to determine ecological differences between the two reservations that would result in the mutually exclusive distribution of the 39 species was narrowed to 7 species, due to the fact that the other 32 were collected only infrequently. The presence at the Natural History Reservation of the artificial pond with its muddy-shore habitat probably accounts for the presence there of *Tipula* (*Y.*) *tricolor, Pilaria imbecilla, P. quadrata,* and *Teucholabis complex,* which were found only there. No such habitat exists at the Breidenthal Reserve. The small, rapid streams with algae- or moss-covered rocks in and along them may explain why *Limonia* (*R.*) *bryanti* and *L.* (*R.*) *lecontei* were found only at the Natural History Reservation. This type of habitat probably also accounts for the fact that *L.* (*G.*) *communis* is abundant in the Natural History Reservation but rare in the Breidenthal Reserve.



TEXT FIGURE 1. Contour map of the Natural History Reservation.



TEXT FIGURE 2. Contour map of the Breidenthal Reserve.

The emergence of adult flies is influenced mostly by local climate. Warm, humid weather in early spring brings vernal species out earlier, while a hot, dry summer delays appearance of autumnal species. As compared to the seasonal distribution of crane flies in southern Michigan, the eastern Kansas population comes out earlier in the spring and disappears later in autumn, due to the longer duration from the last, spring, killing frost to the first, autumnal, killing frost. Several species that have but a single adult season in southern Michigan have two distinct ones in eastern Kansas.

From the preceding study it seems reasonable to draw three conclusions. First, crane flies of eastern Kansas had their origins in the eastern part of the continent. Second, geographical and climatic factors have differentiated the crane fly faunas of eastern Kansas and the more eastern states. Third, mainly topographic and historical factors have influenced the differences in crane fly faunas between the Breidenthal Reserve and the Natural History Reservation.

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APPENDIX

A Key to the Adult Crane Flies of Eastern Kansas

(modified from Alexander, 1942)

1. Terminal segment of maxillary palpus elongate; antennae usually with 13 segments; wings with Sc_1 usually atrophied; body size large (Fig. 1) ..... (Tipulinae) 2

Terminal segment of maxillary palpus short; antennae usually

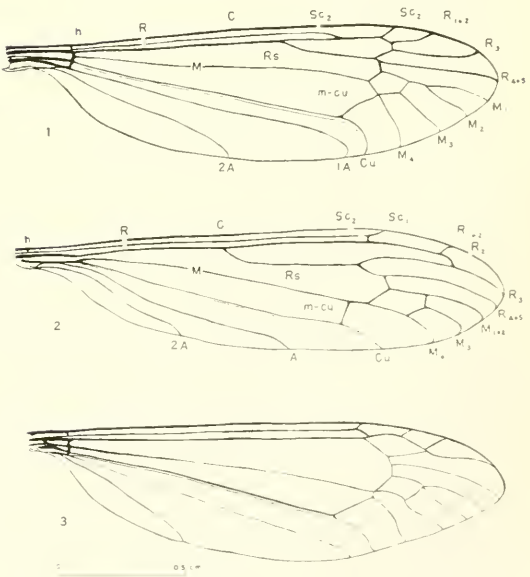

Fig. 1. Wing of *Tipula* (*Lunatipula*) *flavoumbrosa;* A—anal veins, C—costa, Cu—cubitus, M—media, m-cu—median-cubital cross-vein, R—radius, Rs—radial sector, Sc—subcosta. Fig. 2. Wing of *Limonia* (*Limonia*) *cinctipes*. Fig. 3. Wing of *Nephrotoma euceroides*.

with 14 or 16 segments; wings with Sc_1 present; body size small or medium (Fig. 2) ..... (Limoniinae) 41

2. Legs long and filiform, tarsi as long as femur and tibia together; wings with vein R_{1+2} atrophied ..... (*Dolichopeza*) 3

Legs of normal stoutness; wings with vein R_{1+2} present 6

3. Gonapophyses with tips flattened, the apex irregularly toothed (Fig. 4) ..... *Dolichopeza walleyi*

Gonapophyses shaped like small knobs, bearing decurved stout black spines and bristles (Fig. 5) 4

4. Tergal arms (9th abdominal tergum) widely flared and emarginate at tips; teeth of ninth tergum not set close together (Fig. 6) ..... *Dolichopeza obscura*

Tergal arms not flared or emarginate at tips; teeth of ninth tergum set close together on common base 5

5. Three teeth of ninth tergum of nearly equal length (Fig. 7) ..... *Dolichopeza tridenticulata*

Three teeth of ninth tergum with middle tooth the longest (Fig. 8) ..... *Dolichopeza polita pratti*

6. Wings with Rs shorter than m-cu; thoracic dorsum, less often other body surfaces; highly polished (Fig. 3) ..... (*Nephrotoma*) 7

Wings with Rs elongate, exceeding m-cu, body surfaces pruinose or pollinose ..... (*Tipula*) 13

7. Thoracic stripes black 8

Thoracic stripes not black 9

8. Occiput dull; wing-tip clear ..... *Nephrotoma virescens*

Occiput with a polished triangular brand; wing-tip darkened ..... *Nephrotoma alterna*

9. Mesonotum dull ..... *Nephrotoma macrocera*

Mesonotum polished 10

10. Flagellar segments unicolorous ..... *Nephrotoma ferruginea*

Flagellar segments bicolorous 11

11. Stigma dark brown, wing-tips distinctly darkened ..... *Nephrotoma polymera*

Stigma yellowish brown, wing-tips not darkened 12

12. Antennae (male) 19-segmented ..... *Nephrotoma eucera*

Antennae (male) 17-segmented ..... *Nephrotoma euceroides*

13. Outer cells of wings with macrotrichia ..... (subgenus *Trichotipula*) 14

Cells of wings without macrotrichia 15

14. Body color bright polished yellow, reddish and black; antennae short; macrotrichia of cells restricted to cells R_5 and M_1 ..... *Tipula stonei*

Body color dull brown and yellow; antennae of male elongate; macrotrichia in cells R_3 to 2nd M_2 ..... *Tipula unimaculata*

15. Rs long, fully twice m-cu; m-cu uniting with M_{3+4} some distance before fork of latter ..... (subgenus *Nippotipula*) ..... *Tipula abdominalis*

Wings with m-cu inserted at the fork of M_{3+4} or beyond, on base of M_4 16

16. Wings with m-cu long, so that cell M_4 is very deep, much wider at base than at margin ..... (subgenus *Schummelia*) ..... *Tipula hermannia*

Wings with m-cu of moderate length, cell M_4 only a little wider at base than at margin 17

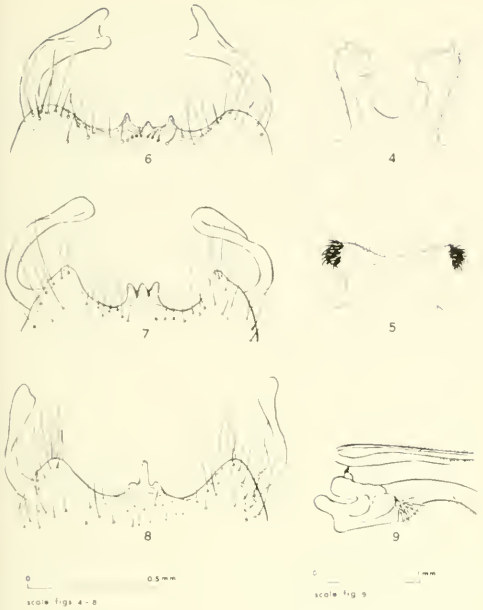

Fig. 4. Gonapophyses of *Dolichopeza* (*Oropeza*) *walleyi*, dorsal aspect. Fig. 5. Gonapophyses of *D.* (*O.*) *obscura*, dorsal aspect. Fig. 6. Ninth tergum of male *D.* (*O.*) *obscura*. Fig. 7. Ninth tergum of male *D.* (*O.*) *tridenticulata*. Fig. 8. Ninth tergum of male *D.* (*O.*) *polita pratti*. Fig. 9. Squama of *Tipula* (*L.*) *duplex*.

17. Male hypopygium with ninth tergum and sternum fused into a continuous ring (Fig. 10) 18
Male hypopygium with the ninth tergum and sternum separated by pale membrane (Fig. 11) 23

18. Wings usually patterned with longitudinal bands, mainly along veins; ninth abdominal tergum of male produced backward as median lobe or pair of lobes bearing small black denticles (Fig. 12) ..... (subgenus *Yamatotipula*) 19
Wings not patterned with longitudinal bands; ninth abdominal tergum of male shallowly emarginate medially (Fig. 13) ..... (subgenus *Platytipula*) 20

19. Wings unmarked except for stigmal darkening and dark costal border; no dark seam on vein Cu and m-cu ..... *Tipula sayi*
Wings longitudinally striped with brown and white; a dark seam on vein Cu and m-cu 20

20. Wings with the cells beyond cord, including R_5, darkened ..... *Tipula tricolor*
Wings with outer portion of cell R_5 white 21

21. Wings with vein 2A bordered by brown ..... *Tipula furca*
Wings with vein 2A not bordered by brown ..... *Tipula strepens*

22. Wings patterned with brown areas in cell M and at outer end of vein 2A ..... *Tipula ultima*
Wings without brown areas; costal border of wings dark brown (Fig. 14) ..... *Tipula paterifera*

23. Squama naked 24
Squama with a small group of setae (Fig. 9) ..... (subgenus *Lunatipula*) 26

24. Male hypopygium elongated, cylindrical, upturned at an angle to remainder of abdomen ....(subgenus *Beringotipula*) .... *Tipula borealis*
Male hypopygium not elongated, not upturned at an angle to remainder of abdomen ..... (subgenus *Pterelachisus*) 25

25. Wing pattern pale; basal section of M_{3+4} shorter than basal section of M_{1+2} ..... *Tipula ignobilis*
Wing pattern heavy; basal section of M_{3+4} subequal to basal section of M_{1+2} ..... *Tipula trivittata*

26. Wings with cell 1st M_2 very small, second section of M_{1+2} shorter than or subequal to petiole of cell M_1 27

Wings with cell 1st M_2 normally elongated, second section of M_{1+2} exceeding petiole of cell M_1 28

27. Second section of M_{1+2} shorter than petiole of cell M_1 .... *Tipula bicornis*
Second section of M_{1+2} subequal to petiole of cell M_1 .... *Tipula morrisoni*

28. Male hypopygium asymmetrical, right basistyle produced caudad into a conspicuous 2-branched arm (Fig. 20) ..... *Tipula fuliginosa*
Male hypopygium symmetrical 29

29. Cells beyond cord of wing darkened 30
Cells beyond cord of wing uniformly colored 31

30. Cells basad of cord strongly infumed ..... *Tipula dorsimacula*
Cells basad of cord uniformly pale in color ..... *Tipula mallochi*

31. Antennae with bases of flagellar segments light yellow, the remainder black ..... *Tipula flavibasis*
Antennae with flagellum, if bicolorous, with bases of segments darker than remainder 32

32. Antennae (male) elongate, if bent backward extending about to fourth abdominal segment .... *Tipula disjuncta*
Antennae (male) shorter, not extending caudad beyond base of abdomen 33

33. Male hypopygium with caudal margin of ninth tergum having two rounded emarginations, one on either side of double median spinous point; eighth sternum with sclerotized teeth (Fig. 16) 34
Male hypopygium without two rounded emarginations on caudal margin of ninth tergum, eighth sternum without sclerotized teeth 37

34. Male hypopygium with median tergal spines long and slender, needle-like (Fig. 16) 35
Male hypopygium with median tergal spines short (Fig. 15) 36

35. Submedian teeth of eighth sternum slender, parallel-side (Fig. 25) ..... *Tipula triplex*
Submedian teeth of eighth sternum broad at base, with narrow,

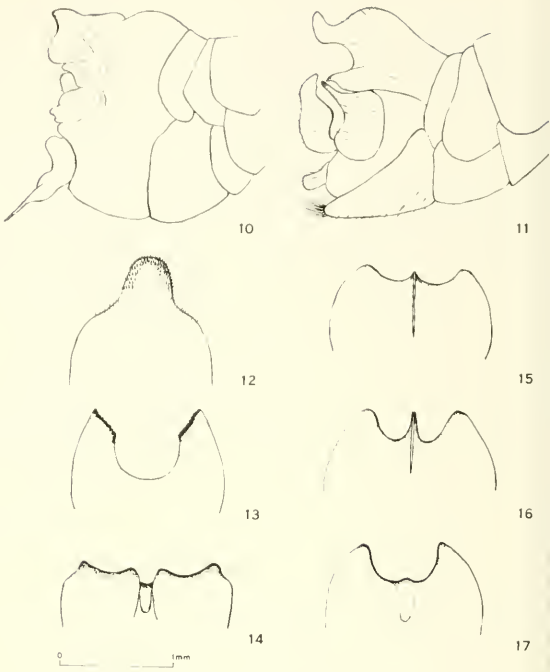

FIG. 10. Ninth segment of male *Tipula* (*Platytipula*) *ultima*, lateral aspect. FIG. 11. Ninth segment of male *Tipula* (*Lunatipula*) *bicornis*, lateral aspect. FIG. 12. Ninth tergum of male *T.* (*Yamatotipula*) *furca*, dorsal aspect. FIG. 13. Ninth tergum of male *T.* (*P.*) *ultima*, dorsal aspect. FIG. 14. Ninth tergum of male *T.* (*P.*) *paterifera*, dorsal aspect. FIG. 15. Ninth tergum of *T.* (*L.*) *flavoumbrosa*, dorsal aspect. FIG. 16. Ninth tergum of male *T.* (*L.*) *triplex*, dorsal aspect. FIG. 17. Ninth tergum of male *T.* (*L.*) *dietziana*, dorsal aspect.

rounded apex (Fig. 26) ..... *Tipula integra*

36. Submedian teeth of eighth sternum triangular in outline, broad basally, narrowed apically (Fig. 27) ..... *Tipula flavoumbrosa*
Eighth sternum having a median depressed lobe arising upside down and slightly cephalad of the submedian teeth (Fig. 28) ..... *Tipula perlongipes*

37. Ground color of mesonotum gray or grayish, pleura light gray 38
Ground color of mesonotum brownish or yellow, pleura yellowish 39

38. Male hypopygium with eighth sternum armed with four conspicuous lobes (Fig. 24) ..... *Tipula australis*
Male hypopygium with eighth sternum bilobed (Fig. 19) ..... *Tipula dietziana*

39. Male hypopygium with lateral lobes of ninth tergum produced into long curved horns (Fig. 18) .. *Tipula tuscarora*
Male hypopygium without curved tergal horns (Fig. 23) 40

40. Outer appendage of inner dististyle elongate, terminating in an acute spine (Fig. 21) .. *Tipula duplex*
Outer appendage of inner dististyle elongate but broad at apex (Fig. 22) ..... *Tipula translucida*

41. Free tip of Sc_2 often present; veins R_4 and R_5 fused to margin, only two branches of Rs being present; antennae usually with 14 or 16 segments (Fig. 2) ..... (*Limoniini*) 42
Free tip of Sc_2 atrophied; veins R_4 and R_5 separate, with three branches of Rs present (exceptions in *Atarba, Elephantomyia, Teucholabis*); antennae usually 16 segments (Fig. 41) 68

42. Wings with vein R_2 lacking ..... (*Helius*) ..... *Helius flavipes*
Wings with vein R_2 present 43

43. Antennae 14-segmented; R_2 basal in position, opposite or not far beyond the level of r-m .. (*Limonia*) 44
Antennae 16-segmented; R_2 far distad of level of r-m ..... (*Dicranoptycha*) 62

44. A supernumerary crossvein in cell 1st A, connecting the two anal veins ..... (subgenus *Discobola*) .... *Limonia annulata*
No supernumerary crossvein in cell 1st A 45

45. Mouthparts and especially the labial palpi lengthened, the rostrum about as long as the combined head and thorax (Fig. 32) ..... (subgenus *Geranomyia*) 46
Mouthparts not conspicuously lengthened, shorter than the remainder of head 47

46. Wings heavily patterned with dark brown, including a series of 4 or 5 large costal areas ..... *Limonia rostrata*
Wings unmarked ..... *Limonia communis*

47. Antennae of males more or less branched; of females simply serrate (Fig. 31) ..... (subgenus *Rhipidia*) 48
Antennae of both sexes simple 50

48. Wings with abundant pale brown or gray dots in all cells ..... *Limonia lecontei*
Wings with the markings larger, confined to vicinity of veins 49

49. Wings with m-cu far before fork of M; antennae with segment 12 and 13 white in color ..... *Limonia domestica*

Wings with m-cu at fork of M; antennae dark throughout ..... *Limonia bryanti*

50. Vein Sc shorter, ending opposite basal one-third of Rs or before .... (subgenus *Dicranomyia*) 51

Vein Sc long, ending opposite midlength of Rs or beyond 56

51. Wing with cell 1st M_2 open by atrophy of m ..... *Limonia immodestoides*

Wing with cell 1st M_2 closed 52

52. Antennae entirely yellow or with basal two segments yellow; body coloration pale yellow or ochre-yellow 53

Antennae dark, brown or black, throughout; body coloration yellowish brown, gray or polished black 54

53. Male hypopygium with the rostral prolongation bifid at apex (Fig. 42) ..... *Limonia divisa*

Male hypopygium with the rostral prolongation extended into a long blackened point (Fig. 47) ..... *Limonia pudica*

54. Femora brown, the tips broadly yellow ..... *Limonia humidicola*

Femora without paler tips 55

55. General coloration of thorax clear gray, male hypopygium with rostral spines originating from enlarged basal tubercles (Fig. 46) .... *Limonia liberta*

General coloration of thorax brown, rostral spines without basal tubercles (Fig. 43) ..... *Limonia haeretica*

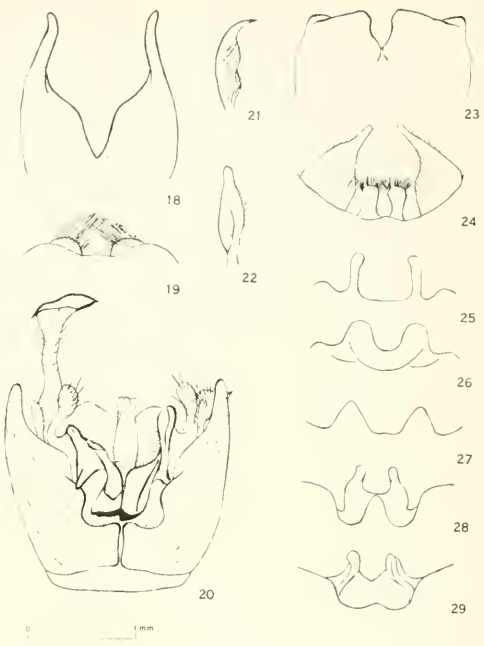

FIG. 18. Ninth tergum of male *Tipula* (*Lunatipula*) *tuscarora*. FIG. 19. Eighth sternum of male *T.* (*L.*) *dietziana*. FIG. 20. Ninth tergum of male *T.* (*L.*) *juliginosa*, dorsal aspect. FIG. 21. Right inner dististyle of male *T.* (*L.*) *duplex*, lateral aspect. FIG. 22. Right inner dististyle of male *T.* (*L.*) *translucida*, lateral aspect. FIG. 23. Ninth tergum of male *T.* (*L.*) *duplex*. FIG. 24. Eighth sternum of male *T.* (*L.*) *australis*. FIG. 25. Eighth sternum of male *T.* (*L.*) *triplex*. FIG. 26. Eighth sternum of male *T.* (*L.*) *integra*. FIG. 27. Eighth sternum of male *T.* (*L.*) *flavoumbrosa*. FIG. 28. Eighth sternum of male *T.* (*L.*) *perlongipes*. FIG. 29. Eighth sternum of male *T.* (*L.*) *triplex* group, species near *perlongipes*.

56. Vein Sc_1 and Sc_2 ending opposite the fork of Rs ..... (subgenus *Metalimnobia*) 57

Vein Sc_1 and Sc_2 ending about opposite midlength of Rs ..... (subgenus *Limonia*) 60

57. Wings yellow, with three subcircular, eye-like brown markings, placed at origin and fork of Rs and at stigma; femora with only one brown band at the tip ..... *Limonia triocellata*

Wings without such an ocelliform

pattern; femora with more than one brown band 58

58. Knobs of halteres uniformly brownish black ..... *Limonia fallax*
Knobs of halteres pale at tips 59

59. Femora with two brown rings, the outer ring narrow and subterminal in position ..... *Limonia cinctipes*
Femora with three brown rings, the outer ring nearly terminal in position ..... *Limonia immatura*

60. Wings unmarked; free tip of Sc_2 lying markedly basad of R_2 ..... *Limonia globithorax*
Wings patterned; free tip of Sc_2 and R_2 in transverse alignment 61

61. R_{1+2} and R_2 subequal in length; legs uniformly dark brown ..... *Limonia rara*
R_{1+2} two or more times as long as R_2; wings with three small brown dots along costal border .... *Limonia tristigma*

62. Fore femora extensively blackened, the bases restrictedly pale; remaining femora more narrowly blackened at tips 63
Femora at most blackened only at extreme tips 64

63. Costal fringe of wings (male) long and conspicuous ..... *Dicranoptycha sobrina*
Costal fringe of wings (male) short and dense ..... *Dicranoptycha megaphallus*

64. Tips of femora narrowly blackened or strongly infumed 65
Femora uniformly pale 66

65. Tips of femora very narrowly dark brown; abdominal terga transversely banded in tigrine color; male with long gonapophyses, bifid near tip ..... *Dicranoptycha tigrina*
Tips of femora broadly blackened; abdominal terga without subterminal dark, transverse bands; male gonapophyses not bifid at tips ..... *Dicranoptycha minima*

66. Body coloration yellow; wing yellow ..... *Dicranoptycha pallida*
Body coloration dark brown; wing grayish to pale brown 67

67. Male hypopygium with aedeagus bifid at apex (Fig. 33) ..... *Dicranoptycha elsa*
Male hypopygium with aedeagus simple (Fig. 34) ..... *Dicranoptycha septemtrionis*

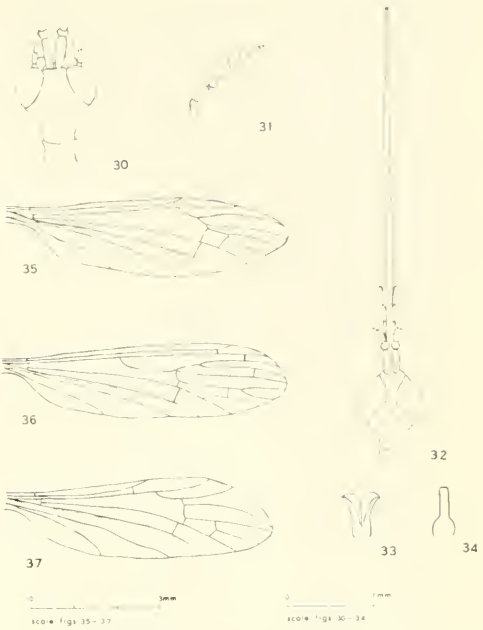

Fig. 30. Head of *Pseudolimnophila luteipennis*, dorsal aspect. Fig. 31. Antenna of *Limonia* (*Rhipidia*) *domestica*, dorsal aspect. Fig. 32. Head of *Limonia* (*Geranomyia*) *communis*, dorsal aspect. Fig. 33. Aedeagus of *Dicranoptycha elsa*, dorsal aspect. Fig. 34. Aedeagus of *D. septemtrionis*, dorsal aspect. Fig. 35. Wing of *Atarba picticornis*. Fig. 36. Wing of *Cladura flavoferruginea*. Fig. 37. Wing of *Gonomyia manca*.

68. Tibial spurs present ..... (tribe Hexatomini) 69
Tibial spurs lacking ..... (tribe Eriopterini) 77

69. Rostrum elongate, exceeding one-half length of entire body ..... (*Elephantomyia*) ..... *Elephantomyia westwoodi*
Rostrum short, not exceeding in length remainder of head 70

70. Wings with two branches of Rs reaching the margin (Fig. 35) ..... (*Atarba*) ..... *Atarba picticornis*
Wings with three branches of Rs reaching the margin 71

71. A supernumerary crossvein in cell C ..... (*Epiphragma*) 72
No supernumerary crossvein in cell C 73

72. Wings with pale brown crossbands; a brown ring at tip of each femur ..... *Epiphragma fasciapennis*
Wings with an irregular pattern of brown; a brown ring before tip of each femur ..... *Epiphragma solatrix*

73. Wings with Sc relatively short, Sc_1 ending before level of fork of Rs; antennae with long, conspicuous verticils; head not conspicuously narrowed behind ..... (*Pilaria*) 74
Wings with Sc longer, Sc_1 ending opposite or beyond level of fork of Rs; antennae verticils not conspicuously long; head strongly narrowed and prolonged behind (Fig. 30) ..... (*Pseudolimnophila*) 76

74. Wings with cell M_1 absent; general coloration of thorax blackish ..... *Pilaria quadrata*
Wings with cell M_1 present 75

75. Thoracic dorsum dark brown to black; antennae of males elongate, exceeding one-half length of body ..... *Pilaria tenuipes*
Thoracic dorsum yellow to brownish yellow; antennae short in both sexes, not extending caudad beyond base of abdomen ..... *Pilaria imbecilla*

76. Thoracic pleura pale, striped longitudinally with dark brown, wings unmarked ..... *Pseudolimnophila contempta*
Thoracic pleura uniform light to dark gray; wings marked with pale brown at stigma and along crossveins ..... *Pseudolimnophila luteipennis*

77. Nearly apterous species; wings smaller than halteres ..... (*Chionea*) ..... *Chionea stoneana*
Fully-winged species 78

78. Wings with cell M_1 present (Fig. 36) ..... (*Cladura*) ..... *Cladura flavoferruginea*
Wings with cell M_1 absent (Fig. 37) 79

79. Two branches of Rs reach wing-margin 80
Three branches of Rs reach wing-margin 82

80. Wings with Sc long, Sc_1 ending beyond origin of Rs ..... (*Teucholabis*) 81
Wings with Sc short, Sc_1 ending before origin of Rs (Fig. 37) ..... *Gonomyia manca*

81. Sc long, Sc_1 ending far beyond midlength of Rs ..... *Teucholabis complexa*
Sc shorter, Sc_1 ending slightly beyond origin of Rs ..... *Teucholabis lucida*

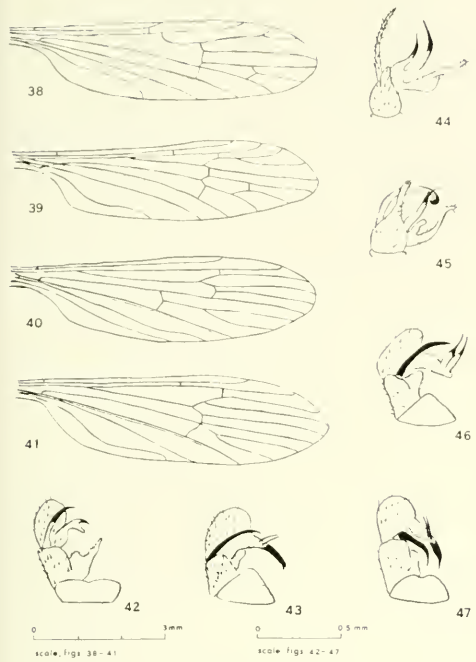

Fig. 38. Wing of *Gonomyia sulphurella*. Fig. 39. Wing of *Ormosia romanovichiana*. Fig. 40. Wing of *Molophilus pubipennis*. Fig. 41. Wing of *Erioptera* (*Erioptera*) *septemtrionis*. Fig. 42. Ventral dististyle of *Limonia* (*Dicranomyia*) *divisa*, dorsal aspect. Fig. 43. Ventral dististyle of *L.* (*D.*) *haeretica*, dorsal aspect. Fig. 44. Inner dististyle of *Gonomyia kansensis*, dorsal aspect. Fig. 45. Inner dististyle of *G. florens*, dorsal aspect. Fig. 46. Ventral dististyle of *L.* (*D.*) *liberta*, dorsal aspect. Fig. 47. Ventral dististyle of *L* (*D*) *pudica*, dorsal aspect

82. Wings with vein R_3 shorter than petiole of cell R_3 ..... (*Gonomyia*) 83
Wings with vein R_3 longer than petiole of cell R_3 86

83. Cell R_3 very small, its extent along costal margin subequal to that of cell R_2 (Fig. 38) ..... *Gonomyia sulphurella*
Cell R_3 large, its extent along costal margin much greater than that of cell R_2 84

84. Wings with cell 1st M_2 closed ..... *Gonomyia subcinerea*
Wings with cell 1st M_2 open, merged with cell M_3 85

85. Male hypopygium with inner arm of inner dististyle bifid (Fig. 44) ..... *Gonomyia kansensis*
Male hypopygium with inner arm of inner dististyle simple, undivided (Fig. 45) .... *Gonomyia florens*

86. Wings with distinct macrotrichia in outer cells 87
Wings with the outer cells glabrous 90

87. Size very small (wings 2.6 mm. or less); cell R_3 sessile, without element R_{2+3+4}; body dark brown ..... (*Tasiocera*) ..... *Tasiocera ursina*
Size larger; cell R_3 petiolate by presence of R_{2+3+4} .... (*Ormosia*) 88

88. Wings with cell 1st M_2 open ..... *Ormosia ingloria*
Wings with cell 1st M_2 closed 89

89. Wings clouded with dark; anal veins convergent (Fig. 39) ..... *Ormosia romanovichiana*
Wings unicolorous ..... *Ormosia arcuata*

90. Rs ending in cell R_3, no element R_{2+3+4} (Fig. 40) .. (*Molophilus*) 91
Rs ending in cell R_1, with short vein R_{2+3+4} present 92

91. Body coloration pale reddish yellow; fore femora extensively blackened, remaining femora yellowish ..... *Molophilus pubipennis*
Body coloration dark brown ..... *Molophilus hirtipennis*

92. Coxae of middle and hind legs only slightly separated by small meral region; knobs of halteres light yellow ..... (*Gnophomyia*) ..... *Gnophomyia tristissima*
Coxae of middle and hind legs widely separated by large meral region ..... (*Erioptera*) 93

93. A supernumerary crossvein in cell R_3; vein 2A strongly sinute ..... (subgenus *Symplecta*) ..... *Erioptera cana*
No supernumerary crossvein in cell R_3 94

94. Wings with anal veins convergent, cell 1st A at midlength usually as broad as, or broader than, at margin (Fig. 41) ..... (subgenus *Erioptera*) 95
Wings with anal veins divergent, cell 1st A widest at margin 96

95. Knobs of halteres dark brown; body coloration brown ..... *Erioptera septemtrionis*
Halteres pale throughout; body coloration pale yellow ..... *Erioptera vespertina*

96. Wings with cell 1st M_2 open ..... (subgenus *Mesocyphona*) 97
Wings with cell 1st M_2 closed 99

97. Wings with a faint brown tinge, the cord and veins at margin with small dark brown spots ..... *Erioptera parva*
Wings with a strong brown tinge, variegated with numerous white spots and dots 98

98. Femora with two brown rings ..... *Erioptera caliptera*
Femora with single brown ring ..... *Erioptera needhami*

99. Wings with a spur from the angulated basal section of vein M_3 jutting basad into cell 1st M_2 ..... (subgenus *Hoplolabis*) ..... *Erioptera armata*
Wings without such a spur ..... (subgenus *Psiloconopa*) 100

100. Wings with two broad brown crossbands ..... *Erioptera venusta*
Wings with dark pattern broken into small spots or narrow broken bands 101

101. Femora with two broad black rings ..... *Erioptera graphica*
Femora with two narrow brown rings ..... *Erioptera armillaris*

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SEXUAL SIZE DIFFERENCES IN THE GENUS *SCELOPORUS*

By

HENRY FITCH

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SEXUAL SIZE DIFFERENCES IN THE GENUS *SCELOPORUS*

Henry S. Fitch

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ABSTRACT

Measurements were accumulated for 53 populations of *Sceloporus*, representing most of the well known species in this large, iguanid genus. Males were larger than females in 33 populations, and average male-to-female length (S-V) ratios varied from 123.9% to 87.7%. Significant trends toward females being larger than males were found in species that: a) produced a large clutch or litter (vs. small clutch or litter); b) produced a single annual clutch or litter (vs. multiple clutches or litters); c) lived in temperate (vs. tropical) climates; d) were small or medium sized (vs. large, with S-V exceeding 60 mm). Less significant correlation was found with phylogenetic groupings (Group II tending to have relatively larger males than Group III); and with mode of reproduction (viviparous species tending to have relatively larger males than oviparous species). Neither habitat (saxicolous, arboreal or terrestrial), nor development of male or female display colors, nor time of maturity (first to fourth year) showed any significant correlations with sexual size differences. Intraspecific variation in size ratios of the sexes was found in each of six polytypic species checked and in three of them (*scalaris, graciosus, occidentalis*) there was geographic shift from the male being the larger in one area to the female being the larger in another.

INTRODUCTION

In the large iguanid lizard genus *Sceloporus,* differences in size between the sexes have been noted by various authors, but no interspecific trends have been shown. In some populations males have been shown to be larger than females while in others this size relationship is reversed. In field studies of *Sceloporus occidentalis* in Oregon, *S. undulatus* in Kansas, *S. malachiticus* and *S. variabilis* in Costa Rica, and *S. jarrovi* and *S. virgatus* in Arizona, I found strikingly different size ratios between the sexes and have investigated these ratios in other species to seek possible causes and correlations for them.

Earlier (Fitch, 1976), I investigated the size relationships of the sexes in 54 mainland populations (representing 45 full species) of the iguanid genus *Anolis* and found a virtual continuum in male-to-female length ratios from 73.5% to 125.4%. Size relationships of the sexes in anoles were found to be strongly correlated with climatic conditions. Those kinds having a short and concentrated annual breeding season, enforced by unfavorably cold or dry weather prevailing for part of the year, have consistently large males, whereas those species living in aseasonal climates of rain forests and cloud forests have the sexes approximately equal in size or have females larger than males.

The *Anolis* study led to an intergeneric comparison of sexual size difference in *Sceloporus* and *Anolis.* These two successful and dominant groups of iguanid lizards often attain high population densities, generating intense competition within and between species. Both are normally territorial, with aggressive behavior and spectacular display organs well developed in males. However, *Anolis* centers its distribution in the tropics and thrives best in humid climates while *Sceloporus* centers its distribution in the warm, temperate zone and thrives best in arid climates. *Anolis* is unique among iguanids in consistently producing a one-egg clutch, laying at brief (and often regular) intervals, with left and right ovaries alternating in production. On the other hand, clutch size varies much among and within *Sceloporus* species, but with nearly always more than one egg and sometimes more than 20. In the more productive species, the capacity of the female as an egg container might be an adaptive character, subject to selection, which would alter the size relationships of the sexes. The majority of *Sceloporus* species are egg-layers, but many of those occurring in montane or northern climates are viviparous and some of the oviparous species have evolved toward viviparity by retaining their eggs until the embryos are partly developed before laying. These diverse reproductive strategies might be expected to affect the size relationships of the sexes.

The Iguanidae are one of the major families of lizards within which it is a general rule that males are larger than females. These lizards often live in open places and are visually oriented. Many kinds maintain territories and there are stereotyped species-specific display movements that serve in part as territorial signals warning away potential rivals. The display organs, often brightly colored or conspicuously marked, are different in different genera (dewlap, belly patches, underside of tail) and can be presented threateningly to potential rivals, but at most other times are either inconspicuous or are completely hidden. Species vary tremendously, both within and between genera, in size of display organ and complexity of display. The female's display organ may be rudimentary or lacking; if present it is nearly always smaller and less conspicuous than the male's. Relative size of the male in different species and genera seems to be correlated with aggressiveness and with size and conspicuousness of the display organ. Atypical iguanids include the predatory *Crotaphytus (Gam-*

belia) wislizenii in which the male is markedly smaller than the female, with no special display organ or behavior, and the solitary, cryptic, myrmecophagous *Phrynosoma* in which the sexes are approximately the same size and display organs are not developed.

METHODS AND MATERIALS

The essential data for this study were the snout-vent measurements of individual adult *Sceloporus* in substantial series. Thirty such series, from 1,973 specimens, were obtained from the collections in the University of Kansas Museum of Natural History. Measurements were available for 14 other series from published literature: Blair, 1960; Burkholder and Tanner, 1974; Cole, 1963; Crenshaw, 1955; Jackson and Telford, 1974; Mayhew, 1963; Mueller and Moore, 1969; Newlin, 1976; Parker and Pianka, 1973; Tanner and Krogh, 1973; Tinkle, 1973 and 1976; and Webb, 1967. Five series of specimens were examined in the Museum of Vertebrate Zoology, University of California collection, and four series of measurements were obtained in the course of my field studies in Kansas, Oklahoma and Costa Rica.

Whereas most of the meaurements were based on preserved museum specimens, those from my own field studies and from several published reports were taken from live lizards that were released after capture. Measurements of live material are not strictly comparable to those of preserved material. Hardening and shrinkage of the latter produced shorter measurements, perhaps several per cent less than would have been obtained from the same individuals in life. However, the length ratios of the sexes were not affected, as each series of specimens measured consisted entirely of either living or preserved animals.

The problem of setting the minimum size limits for males and females has been discussed for *Anolis* (Fitch, 1976) and is similar for *Sceloporus*. Making the state of the gonads the sole criterion would have eliminated much of the available material, collected at times other than the breeding season. Actually, the criteria were somewhat subjective. In each substantial series the distribution of records tended to approximate a normal curve, but usually was somewhat skewed, with more small adults than large adults, and relatively few in the largest size classes. This was due to the fact that size is strongly correlated with age, the largest individuals being the oldest survivors, while the smaller adults include (along with some retarded older individuals) many that are newly matured and have been exposed for a relatively short time to normal mortality factors. Obviously, the composition of any local population varies according to season, depending on the climate. Average adult size is smaller when many newly matured individuals are present and increases as these continue to grow after sexual maturity. Among the series included here are some that are composites, seasonally or geographically or both, and others that are relatively homogeneous. Some authors showing average difference between sizes of the sexes in specific populations may have used different criteria for setting lower limits for adult size. These factors would all tend to increase the variance among populations.

To account for species differences in size disparity of the sexes Wilcoxon 2-sample tests (Sokol and Rohlf, 1969) were used, with the 53 populations ranked according to their ratios and divided into two series that might be expected to differ (Table 2). Tests were somewhat limited by lack of ecological knowledge concerning the species involved. Size of clutch, frequency of clutch, time required to reach maturity, and even oviparous or viviparous habits are unknown for certain species.

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RESULTS

Range of Sexual Size Difference. Table 1 lists the species and populations studied, ranking them in order from the one with the highest male-to-female size ratio (*S. variabilis*) to the one with the lowest (*S. undulatus elongatus*). The ratios range from 123.9% to 87.7% in almost a continuum, but males are larger in 57% and for all series means combined, males average 104% of female length. Males are most often larger than females, being territorial, pugnacious and equipped with bright colors for display, but it is necessary to explain why the female is larger than the male in 43% of the populations and with bulk averaging as much as 1.5 times that of the male. Ten ecological traits, all interrelated, and closely linked with reproductive strategies, were statistically tested, as set forth in

TABLE 1.

POPULATION SAMPLES OF *Sceloporus* RANKED FROM HIGHEST TO LOWEST IN ORDER OF MALE-TO-FEMALE LENGTH RATIO[1]

SPECIES	♂ TO ♀ LENGTH AS PER CENT	MEAN ♂ LENGTH AND RANGE	MEAN ♀ LENGTH AND RANGE	GEOGRAPHIC ORIGIN	SOURCE
variabilis	123.95**	65.78±.46(74-57 in 97)	53.07±.491(68-44 in 157)	Costa Rica	Fitch field rec.
clarki boulengeri	123.66**	104.0±4.50(138-91 in 27)	84.1±1.58(120-72 in 36)	Sonora, Sinaloa	KU
poinsetti	120.04**	116.39±2.56(130-100 in 18)	96.95±1.80(116-86 in 21)	Chihuahua, Coahuila, Texas	KU
magister	119.50**	115.5(140-80 in 42)	96.6(120-80 in 33)	S. Calif., Ariz., N.M., Son.	Parker & Pianka 1973
pyrocephalus	117.55**	62.89±1.02(68-58 in 9)	53.50±.75(60-49 in 12)	Michoacan, Colima, Guerrero	KU
siniferus	116.24**	60.84±.456(67-53 in 32)	52.34±.42(61-48 in 35)	Oaxaca	KU
nelsoni	115.35**	60.15±.79(65-53 in 26)	52.14±.59(58-48 in 21)	Sonora, Sinaloa	KU
cozumelae	115.51**	50.72±.498(60-43 in 57)	45.484±.591(57-41 in 33)	Yucatan	KU
orcutti	110.87**	102(115-90 in 17)	92(106-85 in 77)	S. Calif.	Mayhew 1963
jarrovi	109.75**	78.75±1.53(91-61 in 35)	71.875(86-57 in 33)	Arizona	KU
insignis	108.35**	89.5(99-80 in 10)	82.6±.60(89-80 in 10)	Michoacan, Colima	Webb 1967
clarki	108.20**	102.07±1.11(118-97 in 29)	94.89±1.32(107-88 in 21)	Arizona, Sonora	KU
adleri	108.16**	65.28±1.13(72-59 in 14)	60.36±1.07(66-54 in 14)	Guerrero	KU
smaragdinus	108.00**	67.22±1.50(80-60 in 14)	62.24±1.65(77-55 in 17)	Guatemala	KU
utiformis	107.95*	64.44±1.75(75-58 in 9)	59.70±1.51(66-51 in 10)	Sinaloa, Jalisco, Nayarit	KU
magister	107.87	96 in 11	89 in 21	Utah	Tinkle 1976
teapensis	107.37**	55.87±1.03 (64-46 in 24)	52.04±.668(62-47 in 26)	Veracruz, Oaxaca, Chiapas	KU
mucronatus omiltemanus	105.43**	93.33±1.03(100-85 in 21)	88.53±1.33(100-81 in 17)	Veracruz, Guerrero	KU

TABLE 1.—(*Continued*)

SPECIES	♂ TO ♀ LENGTH AS PER CENT	MEAN ♂ LENGTH AND RANGE	MEAN ♀ LENGTH AND RANGE	GEOGRAPHIC ORIGIN	SOURCE
chrysostictus	105.18*	53.95±.97(62-45 in 81)	51.30±.97(61-44 in 82)	Campeche, Quintana Roo, Yucatan	KU
merriami annulatus	105.18**	47.69±.474(53-42 in 96)	45.34±.284(50-39 in 62)	Chisos Mts. Texas	KU
merriami	104.93**	52.28±.453(61-45 in 60)	49.82±.266(55-44 in 51)	S. Texas	KU
malachiticus	104.81**	79.12±.59(90-67 in 146)	75.490±.44(86-64 in 208)	Costa Rica	Fitch field records
graciosus vandenburgianus	104.70**	60.2±.44(65-55 in 34)	57.5±.47(63-51 in 26)	S. Calif.	MVZ
magister	104.59**	99.40(115-83 in 53)	95.04(107-81 in 57)	S. Nev.	Tanner & Krogh 1973
grammicus disparilis	104.02*	51.26±.540(57-42) in 23)	49.28±.498(54-44 in 32)	Coahuila, Durango	KU
occidentalis biseriatus	103.56**	75.36±.51(84-65 in 97)	72.77±.77(89-65 in 46)	S. Calif., Baja Calif.	MVZ
bulleri	103.07	100.7(116-95 in 10)	97.7(108-91 in 10)	Sinaloa to Jalisco	Webb 1967
taeniocnemis	102.81	71.11±1.11(81-65 in 19)	68.65±1.49(82-60 in 20)	Chiapas, Guatemala	KU
pictus	102.1	48.88±.443(51-47 in 8)	47.86±1.15(52-44 in 7)	Oaxaca, Puebla	KU
scalaris ("aeneus")	101.33	46.10±.709(49-42 in 10)	45.53±.621(53-41 in 23)	Michoacan, Morelos, Mexico, D.F.	KU
spinosus	101.23	88.29±1.67(99-82 in 17)	87.22±1.57(96-77 in 18)	Oaxaca	KU
torquatus	100.85	103.54±1.76(118-98 in 13)	102.67±1.46(110-97 in 9)	Jal., Mich., Mex., D.F., Guan., Agua Cal.	KU
megalepidurus	100.65	45.20±1.26(50-42 in 10)	44.91±.720(48-41 in 11)	Veracruz, Puebla	KU
undulatus consobrinus	98.94	60.31±.704(74-55 in 45)	60.96±.632(71-55 in 46)	Texas, N. Mexico	KU
graciosus	98.00	49.0 in 25	50.0 in 39	S. Utah	Tinkle 1973
formosus	96.90	71.58±1.38(80-64 in 12)	73.88±1.65(80-68 in 8)	Oaxaca	KU

TABLE 1.—(*Concluded*)

SPECIES	♂ TO ♀ LENGTH AS PER CENT	MEAN ♂ LENGTH AND RANGE	MEAN ♀ LENGTH AND RANGE	GEOGRAPHIC ORIGIN	SOURCE
graciosus "gracilis"	96.66**	52.1±.416(61-49 in 85	53.9±.341(63-48 in 76)	Oregon	MVZ
graciosus	95.79**	57.39(63-52 in 106)	59.91(69-53 in 121)	Utah	Burkholder and Tanner 1974
cyanogenys	95.01*	100.73±3.51(116-86 in 8)	105.91±1.44(119-88 in 22)	Texas, Tamaulipas	KU
lundelli	95.01**	90.0±1.47(93-86 in 4)	94.73±2.66(99-91 in 6)	Yucatan	KU
occidentalis occidentalis	94.0**	66.09±.694(72-61 in 23)	70.38±1.44(77-68 in 13)	W. Oregon	MVZ
woodi	94.28**	47.6	50.5	Florida	Jackson and Telford 1974
scalaris "bicanthalis"	94.14**	45.36±.63(50-43 in 14)	48.82±1.33(55-42 in 11)	Veracruz Mexico, D.F.	KU
undulatus tristichus	93.33**	58.58±.72(70-52 in 33)	62.77±.57(75-57 in 53)	Arizona N. Mexico	KU
undulatus hyacinthinus	93.13**	59.82±.59(63-57 in 18)	64.23±.87(67-57 in 11)	Oklahoma	Fitch field records
occidentalis biseriatus	93.00**	73.64±1.18(81-65 in 14)	82.73±1.43(87-72 in 21)	E. Oregon, Idaho	MVZ
undulatus garmani	92.85**	52.22±.37(59-45 in 62)	56.25±.591(68-53 in 44)	Kansas	Fitch field records
undulatus	90.33**	56.05(65-47 in 59)	62.05(70-53 in 35)	Georgia	Crenshaw 1955
undulatus erythrocheilus	89.86**	59.52±.75(65-53 in 21)	66.24±.53(72-60 in 21)	N. Mexico	KU
olivaceus	89.14**	82.9(93-60 in 34)	93.0(107-63 in 107)	Texas	Blair 1960
scalaris	88.84**	45.53±.57(55-40 in 45)	51.25±.36(60-40 in 203)	S. Calif.	Newlin 1976
virgatus	88.43**	52.0(58-48 in 11)	58.8(69-51 in 10)	S. Arizona	Fitch field records
undulatus elongatus	87.70**	63.10±1.09(71-55 in 20)	71.95±1.03(83-65 in 20)	SW Col.	KU

[1] Significant dimorphism assumed where P ≤ 0.05 (one asterisk); two asterisks indicate P ≤ 0.01.

the following sections. Table 2 shows the extent of correlations as revealed by Wilcoxon 2-sample tests. Table 3 shows the relationships of the species studied, and the occurrence of various ecological traits among them.

Phylogeny. Relationships within the genus and to other genera of iguanids are well known through many osteological, morphological, karylogical and behavioral studies (Etheridge 1964; Smith 1939; Cole 1963; Purdue and Carpenter 1972). Smith (1939) separated the 95 species and subspecies of *Sceloporus* which he considered valid into 15 groups of approximately equivalent morphological value. Smith's arrangement was accepted for 35 years, but eventually was revised and extended by Larsen and Tanner (1974 and 1975). They used over 80 characters, including lepidosis, skull morphology, distribution, behavior and karyology, and applied a statistical treatment with Ward's cluster analysis to determine degrees of relationship within the genus and construct dendrograms reflecting them. They divided the genus into three primary groups, each having several subgroups of from one to nine species. Group I, the smallest of the three, with only three subgroups and seven species, was considered to be the most primitive and the most distinct, and in the 1975 publication it was suggested to comprise a separate genus (*Lysoptychus,* Cope 1888). Group II with 20 species and Group III with 30 were each found to consist of five subgroups.

Only one species in my study, *Sceloporus (Lysoptychus) merriami* (with two populations), was a member of Group I, but 13 species of 14 populations represented all the subgroups of Group II, and 19 species with 30 populations represented all the subgroups of Group III. The samples are therefore considered to be representative of the genus, since the species not included are mostly rare and obscure ones.

In a Wilcoxon 2-sample test (Table 2), Group II and Group III are significantly different at the 95% level in sexual size differences, with Group III having relatively smaller males. However, in each group there are species in which males are larger than females, and vice versa. The subgroups show more significant contrasts. The sexes are approximately equal in size, but with males slightly larger in Group I, Subgroup B (*merriami merriami* and *merriami annulatus*) and in Group II, Subgroup A (*grammicus, pictus* and *megalepidurus*). Males are relatively large in Group II, Subgroups B (*pyrocephalus, nelsoni*), D (*siniferus, utiformis*) and E (*variabilis, cozumelae, teapensis,* and *chrysostictus*) and in Group III, Subgroups A (*spinosus coeruleopunctatus, orcutti, clarki clarki, clarki boulengeri* and *magister*—but with the notable exception of *olivaceus*) and D (*jarrovi*). Females are generally larger than males in Group III, Subgroup C (*undulatus* and subspecies, *occidentalis* except near its southern limits, *graciosus* except near its southern limits, *virgatus,* and *woodi*). In Group III, Subgroups B (*lundelli, formosus, adleri, smaragdinus, taeniocnemis,* and *malachiticus*) and D (*torquatus, cyanogenys, bulleri, insignis, mucronatus omiltemanus,* and *poinsetti*) neither sex was consistently larger.

Size of Clutch or Litter. Number of eggs per clutch varied from one (*chrysostictus*) to 19 (*torquatus*) in the specimens examined. Blair (1960) recorded a maximum of 30, laid by a large female of *olivaceus.* Mean clutch size varied from 1.8 in *cozumelae* to 14.3 in *olivaceus.* Clutch sizes of various species and populations are shown in Table 4, some based on published literature, others based on dissections of specimens in the collections of the University of Kansas Natural History Museum. Table 5 shows intraspecific variation in clutch size in the wide-ranging species *graciosus, occidentalis* and *undulatus.*

TABLE 2.

WILCOXON 2-SAMPLE TESTS OF CORRELATIONS IN *SCELOPORUS* POPULATIONS RANKED ACCORDING TO MALE-FEMALE LENGTH RATIOS

DIVISION OF SAMPLES	NUMBERS IN SAMPLES	*t*-VALUES
small brood, mean < 4	33	3.56**
vs.		
large brood, mean > 4	10	
single annual clutch or litter	28	3.36**
vs.		
multiple clutches	14	
tropical	20	2.82**
vs.		
temperate	33	
male, less than 60mm S-V	22	2.60*
vs.		
male, more than 60mm S-V	31	
Group II	14	2.23*
vs.		
Group III	37	
oviparous	36	1.97*
vs.		
viviparous	17	
saxicolous	12	1.75
vs.		
arboreal or terrestrial	35	
female display patches developed	12	1.70
vs.		
female display patches faint or absent	41	
male display patches developed	49	1.34
vs.		
male display patches faint or absent	4	
maturity attained in first year	33	.334
vs.		
maturity attained 2nd to 4th year	18	

** Significant at 99%.
* Significant at 95%.

Species whose reproductive strategy involves producing a large egg-clutch (or litter) may be subject to selective pressure to increase body size of the female as a more capacious egg container. Sexual size difference showed higher correlation with clutch size than with any other factor tested and species producing large clutches or litters tended to have relatively large females. Table 2 shows that 33 populations

TABLE 3
Ecological Traits of Various *Sceloporus* Species

Species	Single or multiple annual clutch or litter	Tropical or temperate climate	Group and subgroup	Oviparous or viviparous	Saxicolous, arboreal or terrestrial	Female display patches	Male display patches	Year of attainment of maturity
adleri	S	Trop.	III B	V	T	No	Yes	1
bulleri	S	Trop.	III E	V	S	Yes	Yes	2+
chrysostictus	M	Trop.	II E	O	T	No	No	1
clarki	M	Temp.	III A	O	A	No	Yes	1
cozumelae	M	Trop.	II E	O	T	No	No	1
cyanogenys	S	Temp.	III E	V	S	No	Yes	2+
formosus	S	Trop.	III B	V	A	No	Yes	1
graciosus	S-M	Temp.	III C	O	T	No	Yes	2
grammicus	S	Temp.	II A	V	A	No	Yes	1
insignis	S	Trop.	III E	V	S	No	Yes	2
jarrovi	S	Temp.	III D	V	S	No	Yes	1
lundelli	?	Trop.	III B	V	A	No	Yes	1
magister	S	Temp.	III A	O	A	No	Yes	2+
malachiticus	S	Trop.	III B	V	A	Yes	Yes	1
megalepidurus	S	Trop.	II A	V	?	No	No	?
merriami	S	Temp.	I B	O	S	Yes	Yes	1
mucronatus	S	Trop.	III E	V	A	No	Yes	2
nelsoni	S	Temp.	II B	O	T	No	Yes	1
occidentalis	S-M	Temp.	III C	O	A	Yes	Yes	2
olivaceus	M	Temp.	III A	O	A	No	Yes	1
orcutti	S	Temp.	III A	O	S	No	Yes	2
pictus	?	Trop.	II A	V	?	No	Yes	1
poinsetti	S	Temp.	III E	V	S	No	Yes	2+
pyrocephalus	?	Trop.	II B	O	T	No	Yes	1
scalaris	S	Temp.	II C	O-V	T	No	Yes	1
siniferus	M	Trop.	II D	O	T	No	Yes	1
smaragdinus	S	Trop.	III B	V	A	No	Yes	1
spinosus	?	Temp.	III A	O	A	No	Yes	?
taeniocnemis	S	Trop.	III B	V	A	No	Yes	1
teapensis	M	Trop.	II E	O	T	No	Yes	1
torquatus	S	Trop.	III E	V	S	No	Yes	2+
undulatus	S-M	Temp.	III C	O	S-A	Some	Yes	1-2
utiformis	M	Trop.	II D	O	T	No	No	1
variabilis	M	Trop.	II E	O	T	No	Yes	1
virgatus	S	Temp.	III C	O	T	No	No	1
woodi	M	Temp.	III C	O	T	Yes	Yes	1

TABLE 4

SIZE OF CLUTCH OR LITTER IN VARIOUS SPECIES AND POPULATIONS OF *Sceloporus*

SPECIES OR POPULATION	MEAN CLUTCH OR LITTER	RANGE	N	COUNTS FROM INDIVIDUAL FEMALES	REGION	AUTHORITY
adleri	3.8	2-6	5	2,3,4,4,6	Guerrero	KU
aeneus (=*scalaris*)	5.22±.428	4-7	9	.....	Michoacan, Morelos, Mexico, D.F.	KU
bicanthalis (=*scalaris*)	6.75	.....	4	.....	Veracruz	KU
chrysostictus	2.43±.466	1-4	16	.....	Campeche, Quintana Roo, Yucatan	KU
clarki boulengeri	8.2	.....	5	4,7,10,10,10	Sinaloa	KU
cozumelae	1.8	.....	12	.....	Yucatan	Maslin 1963
cyanogenys	13.3	6-18	7	.....	S. Texas, Tamaulipas	Hunsaker 1959
formosus	8.0	.....	4	7,7,9,9	Oaxaca	KU
grammicus disparilis	5.7	4-7	7	.....	Veracruz	Werler 1951
jarrovi	6.75±.32	.....	52	.....	S. Ariz.	Tinkle and Hadley, 1973
jarrovi	6.77	.....	85	.....	S. Ariz.	Goldberg 1971
jarrovi	5.37	.....	52	.....	S. Ariz.	Ballinger 1973
magister	6.6	4-10	7	.....	S. Nev.	Tanner and Krogh, 1973
magister	8.4	3-12	14	.....	S.W. states	Parker and Pianka, 1973
magister	6.2	2-9	22	.....	S. Utah	Tinkle 1976
malachiticus	4.5	.....	20	.....	Costa Rica	Fitch 1970
merriami	3.7	2-5	27	.....	S. Texas	Chaney and Gordon, 1954
mucronatus	.....	.....	.....	9	Veracruz	Werler 1951
nelsoni	6.25	.....	4	4,6,7,8	Sonora, Sinaloa	KU
olivaceus	14.3	.....	.....	.....	Texas	Blair 1960
orcutti	11	.....	.....	.....	S. Calif.	Mayhew 1963

TABLE 4.—(*Continued*)

SPECIES OR POPULATION	MEAN CLUTCH OR LITTER	RANGE	N	COUNTS FROM INDIVIDUAL FEMALES	REGION	AUTHORITY
pictus	3.6	.....	5	2,2,4,4,6	Oaxaca, Puebla	KU
poinsetti	10.45±1.01	6-23	40	.....	S.W. Tex.	Ballinger 1973
pyrocephalus	4.66	.....	3	3,4,7	Michoacan, Colima	KU
scalaris	6.22±0.42 1st yr ♀ ♀ 10.54±0.58 2nd yr and older ♀ ♀	.....	49 37		S. Ariz.	Newlin 1976
siniferus	5.0	4-6	4	.....	S. Oaxaca	KU
smaragdinus	4.20±.344	3-6	10	.....	Guatemala	KU
spinosus coeruleopunctatus	12.66	8-16	6	.....	Oaxaca	KU
teapensis	2.33	.....	3	2,2,3	Yucatan Pen.	KU
torquatus	.....	.....	.....	6	Michoacan	Werler 1951
variabilis	3.0	.....	18	.....	Costa Rica	Fitch 1970
virgatus	9.45±2.4	4-16	184	.....	S. Ariz.	Vinegar 1976
virgatus	10.2	5-15	15	.....	S. Ariz.	Cole, 1963
woodi	4.13±.32	.....	.....	.....	Florida	Jackson and Telford, 1974

having small clutches < 4 were significantly different, at the 99% level, in sexual size difference, from 10 populations having large clutches or litters > 4.

Single or Multiple Clutches. Some species in this study are not known to produce either single clutches or multiple clutches, and are omitted. So far as I know, all viviparous species are single-brooded, since gestation extends over several months Oviparous species that are also single-brooded include *graciosus* at high elevations and northern latitudes (Burkholder and Tanner, 1974; Mueller and Moore, 1969); *merriami* (Chaney and Gordon, 1954); *virgatus* (Vinegar, 1975); *orcutti* (Mayhew, 1963); *magister* (Parker and Pianka, 1973); and *occidentalis* (Fitch, 1940; Goldberg, 1974). Species and subspecies known to be multiple brooded include *undulatus undulatus* (Crenshaw, 1955; Tinkle and Ballinger, 1972); *undulatus garmani* and *undulatus hyacinthinus* (Fitch, 1970); *woodi* (Jackson and Telford, 1974); *olivaceus* (Blair, 1960); and *variabilis* (Fitch, 1973). I found that *S. clarki boulengeri, chrysostictus, cozumelae, teapensis, spinosus coeruleopunctatus, siniferus* and *utiformis* all had young in various stages of growth at different times of year, indicating a long breeding season and multiple clutches.

The species known to be single-clutched, when arrayed against those known to have multiple clutches, and subjected to a Wilcoxon 2-sample test for correlation with sexual size difference (Ta-

TABLE 5

CLUTCH SIZE IN VARIOUS POPULATIONS OF *SCELOPORUS GRACIOSUS, S. OCCIDENTALIS* AND *S. UNDULATUS*

SPECIES	MEAN CLUTCH	RANGE	N	REGION	AUTHORITY
graciosus "gracilis"	3.6	.....	32	Oregon, N. Calif.	Fitch, 1970
graciosus graciosus	6.03	2-10	143	N. Utah	Burkholder and Tanner, 1973
graciosus graciosus	3.8	.....	72	S. Utah	Tinkle, 1973
graciosus vandenburgianus	4.24	.....	25	S. Calif., Baja Calif.	Fitch, 1970
occidentalis occidentalis	7.8	.....	14	W. Oregon	Fitch, 1970
occidentalis occidentalis	11.3±.41	.....	.....	Central Sierra, 1500 m	Jameson and Allison, 1976
occidentalis occidentalis	13.4±.57	.....	.....	Central Sierra, 2200 m	Jameson and Allison, 1976
occidentalis longipes	11.2	7-14	15	S. Nevada	Tanner and Hopkin, 1972
occidentalis biseriatus	7.65	3-14	37	S. Calif., Baja Calif.	Fitch, 1970
occidentalis biseriatus	7.95	.....	84	Los Angeles Co., California	Goldberg, 1973
occidentalis biseriatus	7.23	.....	43	Whittier, California	Goldberg, 1974
occidentalis biseriatus	8.70	.....	41	San Gabriel Mts., Calif.	Goldberg, 1974
occidentalis biseriatus	8.56	.....	9	E. Oregon, Idaho	Fitch unpublished (MVZ specimens)
undulatus undulatus	7.6	.....	.....	Georgia	Crenshaw, 1955
undulatus undulatus	7.4±.26	.....	.....	S. Carolina	Tinkle and Ballinger, 1972
undulatus consobrinus	6.2	3-8	13	Oklahoma	Carpenter, 1959
undulatus elongatus	6.3±.18	.....	.....	Utah	Tinkle, 1972
undulatus erythrocheilus	9.0	4-13	6	Oklahoma	Carpenter, 1959
undulatus garmani	7.6	5-12	10	Oklahoma	Carpenter, 1959
undulatus hyacinthinus	11.8±.47	.....	.....	Ohio	Tinkle and Ballinger, 1972

TABLE 6

Trend of Decreasing Male-to-Female Size From Warm to Cool Climate

Climatic zone	Mean male-to-female range length as percentage	Populations sampled N
Tropical lowlands	109.02 (93.3-130.8)	10
Tropics (both lowland and montane)	106.22 (93.3-130.8)	19
Tropical montane	103.11 (96.9-108.2)	9
Temperate zone (all samples)	100.20 (87.3-123.7)	34
Temperate (USA)	99.15 (94.3-120.1)	29
Temperate (USA excluding southern tier of states)	94.82 (87.7-107.9)	13

ble 2), showed correlation significant at the 99.9% level. The single-clutch species have relatively small males and large females.

Climate. *Sceloporus* occurs from about 48° 30′ N near the Canadian border in Washington south through much of the continental United States, Mexico and Central America to about 9° N in Panama. Hence, its local populations are adapted to a wide range of climates from those with long, intensely cold winters and short summers to those with hot, aseasonal climates, or those with extreme, desert conditions. Warm, dry conditions are optimum, however, since many species and individuals occur in the arid, southwestern United States and adjacent Mexico.

Seasonal schedules, and reproductive strategies obviously are much altered by climatic factors. Table 6 shows a well-defined trend from relatively small males in cooler climates to relatively large males in the hot climates of tropical lowlands. In Table 2, with 20 mainly tropical species arrayed against 33 species from temperate North America, males tend to be relatively small in the Temperate Zone, with correlation significant at the 99% level.

Body size. Adults of *Sceloporus* ranged from 39 mm S-V in female *S. merriami annulatus* to 138 in male *S. clarki boulengeri,* with means ranging from 45.2 in male *megalepidurus* to 105.9 in female *cyanogenys.* Most populations studied were in the lower size brackets with decreasing numbers toward the upper limits. The 22 smallest species (male S-V averaging less than 60 mm) when arrayed against the 31 largest (averaging more than 60 mm) were found to be significantly different (slightly below the 99% level, see Table 2). Species of small body size tend to have relatively large females. With the ten largest species (those exceeding 90 mm) arrayed against the remaining 43, difference in sexual size dimorphism was somewhat less significant (t=1.78).

Oviparity or Viviparity. The oviparous state, primitive for the suborder Sauria and the family Iguanidae, persists in the majority of species of *Sceloporus,* but many in montane habitats and some that are not montane have become viviparous. Still others have progressed toward viviparity by retaining eggs during part of their development.

Viviparous species include *torquatus* (Mulaik, 1946), *poinsetti* (Ballinger, 1973), *cyanogenys* (Crisp, 1964), *mucronatus omiltemanus* (Davis and Dixon, 1961), and by inference their near relatives in Group C, Subgroup E, *bulleri* and *insignis, jarrovi* (Ballinger, 1973), *malachiticus* (Fitch, 1970; Marion and Sexton, 1971)

and by inference the near relatives of *malachiticus: formosus, smaragdinus, taeniocnemis* and *lundelli; aeneus* in part of its range (Thomas and Dixon, 1976), *grammicus disparilis* (Davis and Dixon, 1961; Mulaik, 1946), *pictus* (Smith and Savitsky, 1974) and *megalepidurus*. Other species are, so far as I know, oviparous.

The oviparous species, arrayed against the viviparous, show a tendency to have males smaller than females, but with the difference not significant at the 95% level (Table 2).

Habitat. The species of *Sceloporus* occur in a spectrum of habitats, terrestrial, arboreal and rocky. However, the genus is generalized, rather than highly specialized for any of these habitat types. There are some euryecic species that occur in a variety of habitats. *S. undulatus,* especially, has populations adapted to diverse habitats, including terrestrial (*garmani*), arboreal (*hyacinthinus*) and saxicolous (*elongatus*), without conspicuous morphological adaptations. In general, the terrestrial species are fine-scaled, with bodies, scales, and limbs slender and tapered, whereas arboreal and, especially, saxicolous species tend to be coarse-scaled with relatively short and thick bodies and appendages. The terrestrial species are swift runners, but scansorial species are less active and depend more on cryptic patterns and behavior and on secure hiding places in cavities and crevices.

In 22 populations considered mainly arboreal, male-to-female length ratio was most often nearly equal (mean 101.7%), with male superiority greater in 12 populations considered mainly saxicolous (mean 103.8%) and 20 populations considered mainly ground-living (mean 105.6%). None of these three groups differed statistically from the others to a significant degree. The kinds considered to be mainly saxicolous (*bulleri, cyanogenys, insignis, jarrovi, merriami, orcutti, poinsetti, torquatus* and the subspecies *elongatus* and *erythrocheilus* of *undulatus*) were most deviant from others in sexual size difference, but with difference not significant at the 95% level.

Display Patches. Brightly colored (usually deep blue) display patches are present on the chin and on the sides of the belly in the males of most species. These patches are either lacking in the female, or are barely discernible as slightly darkened areas without bright color, or if they are colorful they are paler than those of the male and less extensive in area. Even though having some display color, the female may lack either the lateral body patch or the chin patch.

Female iguanid lizards, including *Sceloporus,* are known to perform the stereotyped bobbing display of their species. Even for those that lack colorful display areas, movements may nevertheless serve for territorial assertion, or may function in species-recognition and sex-recognition.

Even within one sex in a local population, development of colored display patches may vary, being present in some, faint or absent in others, so the following groupings are somewhat arbitrary.

Females of *malachiticus, clarki, merriami* (2 populations), *bulleri, woodi, occidentalis* (3 populations) and in *undulatus* the subspecies *elongatus, erythrocheilus* and *tristichus,* have colored display patches more or less developed; in other populations female display colors are absent. In males, only *chrysostictus, cozumelae, utiformis* and *virgatus* lack bright ventral display colors. Table 2 shows that presence or absence of display colors in either sex are not strongly correlated with sexual size difference, but there seems to be some tendency for display colors to develop in females of those species where the females are relatively large.

Time Required to Mature. A combination of innate physiological traits and environ-

mental factors affects rates of development and time required to reach maturity. This time varies in different populations, from three months to three years or more. Actual records of individuals, based on mark and recapture, are available for few populations, but well defined age-size cohorts are observable in some. In general the species are either early maturing (at age of one year or less) or late maturing (in second year or later).

The late maturing species include those of Group III, Subgroup E, *torquatus, cyanogenys* (Crisp, 1964), *poinsetti* (Ballinger, 1973) and by inference their near relatives *bulleri, insignis* and *mucronatus; graciosus* (Mueller and Moore, 1969; Tinkle, 1973), *magister* (Tanner and Krogh, 1973; Tinkle, 1976), *orcutti* (Mayhew, 1963), *occidentalis, clarki* and *undulatus,* subspecies *elongatus tristichus* and *erythrocheilus* (Fitch, 1970). So far as I know, all others are early maturing, but *megalepidurus* and *spinosus coeruleopunctatus,* being little known, were not included in the comparison. No correlation between early or late maturity and relative sizes of the sexes is indicated (Table 2).

Geographic Variation. Geographic variation in sexual size difference was found in all six species for which intraspecific comparisons were made. Seven subspecies of *Sceloporus undulatus* were tested and compared. Females were larger in all of them, but the male-to-female length ratio varied from 87.70% (*elongatus*) to 98.94% (*consobrinus*). Three populations of *S. occidentalis* were compared. In *S. occidentalis occidentalis* of western Oregon, and *S. occidentalis biseriatus* of the same latitude in eastern Oregon and Idaho, males were smaller than females—89.16% and 87.73%. However, in *S. o. biseratus* of southern California and Baja California males were slightly larger than females, 103.56%. A parallel trend was found in populations of *S. graciosus;* in northern *S. g. graciosus,* from western Oregon and northern California, Yellowstone National Park, and Utah County, Utah, males were smaller than females (96.66, 98.00 and 95.79%, respectively). However, in *S. g. vandenburgianus* of southern California, males averaged slightly larger than females (104.69%). Thus, the intraspecific trends of the wide-ranging *occidentalis* and *graciosus* in sexual size differences parallel interspecific trends for the genus as a whole.

Comparison of Species Having Small Female (variabilis) with One Having Large Female (olivaceus). Through Blair's study (1960) *S. olivaceus* of southern Texas is ecologically the best known species of *Sceloporus* by far. It is near the extreme of species having relatively large females (1.12 times male length). Most other species that have been subjects of intensive field studies, including several of the subspecies of *undulatus* (Crenshaw, 1955; Tinkle, 1972; Tinkle and Ballinger, 1972), *occidentalis* (Fitch, 1940; Tanner and Hopkin, 1972), *graciosus* (Tinkle, 1973; Tanner and Krogh, 1973; Mueller and Moore, 1969), *virgatus* (Vinegar 1975), and *woodi* (Jackson and Telford, 1974) are also among those with relatively large females, and available information suggests that, in general, their ecology and social systems are similar to those of *olivaceus.* There are no comparable studies of the species with relatively large males.

For *olivaceus,* Blair (1960) found no well-defined territories, but each adult male had a home range with a principal station and an average of 8.5 additional stations among which he distributed his time. The stations were on trees, fence posts, or other objects on which the lizards could climb. They used intervening open areas only in crossing from one station to another. Home ranges overlapped extensively and the same station might be used by two or more males, but usually both

TABLE 7

DEMOGRAPHIC TRAITS CONTRASTED IN *Sceloporus olivaceus* AND *Sceloporus variabilis*

	S. OLIVACEUS	S. VARIABILIS
Sex ratio in numbers of adults, ♂ to ♀	1 to 1.73	1 to 1.22
mean ♀ home range, m^2	275	326
mean ♂ home range, m^2	684	580
♀ to ♂ length ratio	1 to .89	1 to 1.24
♀ to hatchling length ratio	1 to .29	1 to .432
mean clutch size	14.3	3.0
number of clutches annually	3	> 3
minimum time from hatching to maturity (months)	10	4

were not present simultaneously. When two met at the same station, they fought, with one being driven off temporarily. Blair described mating as promiscuous, but his narrative account indicated that "consort pair" associations were frequent. The male might spend periods of days in close association with a temporary mate, whether or not she was sexually receptive. However, the male's range was 2.3 times that of the female's, and by shifting from one station to another he might associate with a succession of females that overlapped his range. The females were far more tolerant of one another than were the males. Often, two shared a station and Blair witnessed a female-female chase on just one occasion. In *olivaceus* the male's display patches on each side of the abdomen are small and narrow. In the female they may be absent, or when present are smaller and paler than the male's.

At the other extreme, *variabilis* is the species with greatest sexual size difference and relatively large males (1.24 times female length). Clues concerning the significance of relatively large males vs. relatively large females could no doubt be obtained by comparing ecological and behavioral data of *olivaceus* and *variabilis*. My field study of *variabilis* in Costa Rica, 1967-1970 (Fitch, 1973) did not include intensive observation of individuals, but more than 1000 lizards were individually marked and 374 were recaptured after substantial intervals. Some facts concerning the general ecology and social system of *variabilis* were obtained.

Table 7 contrasts some traits of the species *olivaceus* and *variabilis*. Significant facts revealed concerning *variabilis* are that: 1) It occurs in extremely high population densities, especially on the coast along the upper beach. In early December 1967, there were three adult males, six adult females and 52 immatures living within a 10 m radius. Four months later, in the dry season, the same area was occupied by six adult males, nine adult females and four immatures. 2) Where density is high, with ranges of many individuals including adult males, overlapping, there are not discrete territories. 3) Male display, fighting and pursuit is prominent behavior. 4) Male-female associations are common, but ephemeral. 5) The preferred habitat is seral, subject to continual successional change and to gross disturbance. On the beach, especially, favorite stations or lookouts and even the lizards themselves may be swept away in the tide and dropped at new locations (Fitch, 1973). Instability characterizes the habitat and the local population.

DISCUSSION

The relative body sizes of adult males and females in *Sceloporus* vary widely, males averaging approximately 24% longer than females at one extreme, and 12.5% shorter than females at the other extreme. In any population, the size relationship of the sexes depends on the interaction of many selective factors. The equilibrium is easily altered and even within a species local populations differ in the size ratios of the sexes.

The ecological factors that determine size ratios between the sexes in *Sceloporus* are probably somewhat different from those acting on any other group of animals. For instance, in birds and mammals and some lower vertebrates parental care of young is an important aspect of behavior, and in predatory kinds the female often protects the young against the potentially cannibalistic male. In such cases as the spotted hyena (Kruuk, 1972), and various raptorial birds (Hill, 1944; Earhart and Johnson, 1970; Mosher and Matraz, 1974) it is therefore advantageous for the female to be larger than the male. In *Sceloporus* cannibalism is rare, as these lizards are mainly insectivorous. There is no maternal care. Social behavior is primitive and does not involve family ties or group activities. A male and female may intimately associate, whether or not the female is sexually receptive. The male may habitually interact with a neighbor along a territorial boundary and he may tolerate in his territory various non-rivals, including females, juveniles and subordinate, but sexually mature, males. Presumably, any departure from parity in the sizes of the sexes permits some partitioning of food resources (Amadon, 1959; Mills, 1976; Reynolds, 1972; Selander, 1966; Verner and Willson, 1969) and the greater the size difference the smaller the overlap. Whichever sex is smaller is subject to competition from immatures. In the more prolific species, such competition might be severe at certain seasons. Larger size of the female may promote successful reproduction by relieving her of competition, both from the male and from immatures, and by permitting her to dominate the male when heterosexual competition does occur.

Compared with the diversity in anole dewlaps, the colored, ventral display areas of *Sceloporus* show remarkably little interspecific variation. The color patch on the chin, usually blue, may or may not be divided into distinct left and right portions, and may or may not be connected with the belly patches of the same color. In most species the belly patches on the two sides are separated by a paler mid-ventral area, but in old individuals of some kinds, black inner margins of the patches encroach and may fill the intervening space. In most species the dorsal color is cryptic, dull-brown or gray with streaks and spots, and with a paired series of darker transverse blotches on the back which are more prominent in juveniles and females than in adult males. In the latter, the ground color is darkened and the original markings become obscure, but when the animal is warm and active, a pale bluish or greenish area may show at the base of each scale. In the excitement of courtship or territorial defense, the colored dots expand so much that the male becomes gaudy and conspicuous and the entire body is involved in the display. Under most conditions, the belly patches are hidden as the lizard sprawls on the substrate, or raises its body only slightly in crawling and running, although the chin color may be visible from front or lateral view. However, when the lizard displays, it stands high and flattens the body in a vertical plane, puffs out the throat and turns sideways to an opponent, presenting its ventral colors conspicuously.

It might be expected that in *Sceloporus* species having relatively large males these

would have: 1) well developed display patches and display behavior, 2) aggressive behavior, combat, and maintenance of well-defined territories and 3) mating systems that usually do not involve enduring pair associations, but are promiscuous or polygynous, with maintenance of leks or harems. Conversely, in species having the male smaller than the female, or near her size, he might be expected to have less prominent display, less tendency for combat and territoriality, less capacity to dominate the female, and a mating system that involes more enduring pair associations instead of harems or leks. Actually, too little is known of behavior in free-living *Sceloporus* to judge the extent of these correlations. The correlations that have been found involve traits of the female, rather than those of the male.

In mainland *Anolis,* those species living in relatively dry climates and having relatively short and concentrated breeding seasons all had males relatively large compared with females (Fitch, 1976). In contrast, those species living in relatively aseasonal climates of cloud forests or rain forests either have the sexes approximately equal in size, or have the females larger. This trend was explained by the more intense competition between males for territories and mates in the stress of a concentrated breeding season, resulting in selection for large size and aggressiveness.

Size relationships of the sexes in *Sceloporus* are not determined by the same set of factors that control them in *Anolis.* In fact, the climatic factors that generate relatively large males in *Anolis* were found to produce relatively large females in *Sceloporus.* The key to this difference seems to lie in the consistent single egg of *Anolis* versus the variable and often large clutch of *Sceloporus.* In a severely seasonal climate that limits breeding to a brief annual interval of optimum conditions, with a single clutch, there is a premium on making the clutch as large as possible. Number of eggs can be increased by making the individual eggs smaller. This has been accomplished in some instances, but, in general, the smaller the hatchling the poorer would be its chances of survival. The alternative strategy is to increase the female's capacity to produce and contain eggs by increasing her size. All the correlations with sexual size difference that were found seemed to hinge on the female's egg capacity.

There is strong support for the idea that relatively large size of the female is correlated with single broodedness, and with clutch size, in the intraspecific trends of several wide-ranging species. At the latitude of Oregon, *S. occidentalis occidentalis* and *S. o. biseriatus* which produce only one large clutch per season and require two years for the young to mature, have relatively large females (male-to-female ratio 94.0% and 93.0% respectively), but in southern California, where smaller clutches and more than one clutch are laid annually (Goldberg, 1974) with some young maturing in the first year, *biseriatus* females are relatively smaller (male-to-female ratio 103.66%). Jameson and Allison (1976) found that, in the central Sierra Nevada of California, female *occidentalis* average 2.5 mm longer at 2200 m than at 1500 m, with mean clutch size of 11.3 eggs at the lower altitude and 13.4 eggs at the higher. (They stated that the size difference between the sexes was greater at the higher altitude, but did not include figures showing male sizes.) Similarly, the small subspecies of *S. undulatus* that occur in the southern and eastern states generally produce three or more clutches annually and have males 90% or more of female length, whereas the large western subspecies, *erythrocheilus* and *elongatus,* produce only one or two clutches and have relatively smaller males (89.85 and 87.70% of female length respectively). Variation in sexual size difference is to be

expected in each subspecies that occurs over a wide climatic range, altitudinally or latitudinally. In northern, single-clutched populations of *S. graciosus* females are larger than males (male-female ratio 95.79%, 96.66% and 98.0%), but in southern California the males are larger than females (104.70%) and presumably females of this population produce at least two clutches annually as Tinkle (1973) has demonstrated in those of southern Utah.

CONCLUSIONS

In 53 populations of *Sceloporus* studied, the size relationships of the sexes varied, in a virtual continuum, from relatively large males at one extreme (123.9% of female length), to relatively small males at the other extreme (87.70% of female length). Males averaged larger in 33 populations and females averaged larger in 20; for the whole group male length averaged 102.8% of female length. Sexual size difference was found to be significant at the 99% level in 42 of the 53.

The size relationships of the sexes are controlled by a complex of factors, including those of reproductive strategy, and also including social structure. Males are more aggressive than females. In most species they maintain territories by displays of colorful ventral patches and actual fighting. However, field studies of behavior under natural conditions are few and it is not yet possible to make interspecific comparisons in such traits as size and permanence of territory, permanence of association between the sexes, extent of male dominance and prevalence of polygyny. These traits are probably correlated with the relative size of the male.

The more significant correlations revealed the high female-to-male size ratio in large-brooded and single-brooded species, as contrasted with those producing small and/or multiple broods. Presumably, in the large-brooded and single-brooded species, the capacity of the female as an egg container is at a premium and there is selective pressure for her size to increase. The next strongest correlations, both above the 99% level, were those of relatively large females in temperate (as contrasted with tropical) climates and relatively large females in small or medium-sized species (as contrasted with large species, of more than 100 mm S-V). In tropical climates, breeding seasons are lengthened and reproductive effort is less concentrated than in temperate climates; the trend parallels that of multiple brooded vs. single-brooded populations. Perhaps in small species, the female's capacity as an egg container is at an even greater premium.

Weaker correlations (significant at the 95% level but not at 99%) were found between sexual size difference and the two major phylogenetic groups, and also between sexual size difference and oviparity vs. viviparity. Possible weak correlations (not significant at the 95% level) were found between sexual size difference and habitat (rock-living vs. tree- or ground-living) and between sexual size difference with large females and development of female display colors. No indication of correlation with sexual size difference was found for development of male display colors, or for time required to mature (first year vs. second to fourth year).

Intraspecific variation in sexual size difference was found in several species, notably the wide-ranging polytypic *undulatus, occidentalis* and *graciosus*. In each of these, the geographic trend paralleled that for the genus as a whole, with northern populations and those at high altitudes having relatively large females.

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A COMPARATIVE ANATOMICAL STUDY OF MANDIBULAR STRUCTURE IN BEES

By
CHARLES D. MICHENER
and
ANNE FRASER

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A Comparative Anatomical Study of Mandibular Structure in Bees[1] (Hymenoptera: Apoidea)

Charles D. Michener and Anne Fraser

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ABSTRACT

Mandibular structures, particularly the ridges and grooves of the outer and inner surfaces, were investigated and illustrated for all major groups of Apoidea. A nomenclature is provided for these structures, and homologies among apoid groups are indicated. A basic mandibular type is found among sphecoid wasps, all short tongued families of bees, and also the Anthophoridae and Fideliidae. Various modifications are found within some of these groups, such as the parasitic anthophorids, the Hylaeinae and Xeromelissinae, and the Xylocopinae. Markedly modified mandibles characterize the Megachilidae and the Apidae.

INTRODUCTION

The taxonomic literature on bees contains many descriptions and illustrations emphasizing the distal parts of mandibles —the apical margins and teeth. These are features whose form is easily seen if the mandibles are open and whose functions are sometimes obvious, e.g., cutting edges

[1] Contribution number 1663 from the Department of Entomology, The University of Kansas, Lawrence, Kansas 66045, U.S.A.

on mandibles of females of leaf-cutter bees (*Megachile*) or multidentate apices of mandibles of those anthidiine bees (e.g., *Anthidium*) that makes their nests with plant hairs. The present paper is not primarily concerned with these features, but deals instead with the surfaces, ridges, and grooves of the mandible, i.e., the body of the mandible. In general, the mandibular body is more conservative than the apical teeth, showing less diversity among species and related genera. A few authors have used the ridges and grooves taxonomically, but in the absence of an overview, no homologies among diverse groups have been apparent and no standard terminology exists.

The object of the study here reported was to establish homologies and terminologies for the parts of the mandible, to facilitate their study, and to look for characters that might illuminate the relationships among major groups of bees.

MATERIALS

The mandibles of many bees were examined in the course of this study. Generally, mandibular structures are better developed in females than in males; detailed analysis was therefore based on females except as noted. From among the many mandibles studied, those of the species listed in Table 1 were selected as representative of most of the variation in the pattern of ridges and grooves and many of them were diagrammed (outer and inner views) as indicated in the table by references to figures.

Species with bizarre swellings or projections are excluded from those illustrated, for they do not contribute to the understanding of the basic structures. However, once the latter are identified, it is often possible to see that a given projection is an elaboration of a particular ridge or interspace.

Letters corresponding to the abbreviations in the figures are given after the names of the structures, where the word or expression is defined in the following section and also in a tabular summary at the end of that

TABLE 1

SPECIES STUDIED.

FAMILY COLLETIDAE
- Subfamily Colletinae
  - *Colletes inaequalis* (Fig. 2)
  - *Leioproctus herbsti*
  - *Callomelitta antipodes* (Fig. 3)
- Subfamily Diphaglossinae
  - *Diphaglossa gayi* (Fig. 4)
  - *Ptiloglossa guinnae*
- Subfamily Hylaeinae
  - *Hylaeus rugosulus*
  - *Amphylaeus morosus* (Fig. 5)
- Subfamily Xeromelissinae
  - *Chilicola ashmeadi* (Fig. 6)
- Subfamily Stenotritinae
  - *Ctenocolletes smaragdinus*

FAMILY HALICTIDAE
- Subfamily Halictinae
  - *Halictus ligatus, quadricinctus* (Fig. 7)
  - *Lasioglossum imitatum, lustrans, texanum, zephyrum*
  - *Pseudaugochloropsis graminea*
  - *Augochlora pura*
  - *Megalopta genalis*
- Subfamily Nomiinae
  - *Nomia melanderi*
- Subfamily Dufoureinae
  - *Dufourea marginata*
  - *Systropha curvicornis*

FAMILY ANDRENIDAE
- Subfamily Andreninae
  - *Andrena accepta* (Fig. 8), *illinoiensis*
- Subfamily Panurginae
  - *Panurginus occidentalis* (Fig. 9)
  - *Panurgus calceatus*
  - *Psaenythia bergi*
  - *Perdita chihuahua*

FAMILY OXAEIDAE
- *Protoxaea gloriosa* (Fig. 10)

FAMILY MELITTIDAE
- Subfamily Melittinae
  - *Melitta leporina* (Fig. 11)
- Subfamily Dasypodinae
  - *Dasypoda panzeri*
- Subfamily Macropidinae
  - *Macropis labiata*
- Subfamily Ctenoplectrinae
  - *Ctenoplectra fuscipes*

TABLE 1—(*Concluded*)

FAMILY ANTHOPHORIDAE
- Subfamily Anthophorinae
  - *Exomalopsis zexmeniae*
  - *Tapinotaspis coerulea*
  - *Ancyloscelis apiformis*
  - *Diadasia enavata*
  - *Melitoma segmentaria*
  - *Anthophora occidentalis* (Fig. 12)
  - *Clisodon terminalis* (Fig. 13)
  - *Svastra atripes* (Fig. 14)
  - *Melissodes agilis*
  - *Centris poecila* (Fig. 15)
  - *Ericrocis lata* (Fig. 16)
  - *Mesoplia garleppi*
  - *Thyreus ramosa* (Fig. 17)
  - *Xeromelecta californica*
- Subfamily Nomadinae
  - *Nomada annulata* (Fig. 18)
  - *Triepeolus concavus*
  - *Biastes brevicornis* (Fig. 19)
- Subfamily Xylocopinae
  - *Macrogalea candida* (Fig. 20)
  - *Allodape mucronata* (Fig. 21)
  - *Ceratina dupla* (Fig. 22)
  - *Manuelia gayi* (Fig. 23)
  - *Xylocopa virginica* (Fig. 24)

FAMILY FIDELIIDAE
- *Fidelia villosa* (Fig. 25)
- *Neofidelia profuga* (Fig. 26)

FAMILY MEGACHILIDAE
- Subfamily Lithurginae
  - *Lithurge gibbosus* (Fig. 29)
- Subfamily Megachilinae
  - *Paranthidium jugatorium*
  - *Dianthidium ulkei*
  - *Callanthidium illustre*
  - *Anthidiellum notatum* (Fig. 27)
  - *Anthidium manicatum* (Fig. 28)
  - *Parevaspis carbonaria*
  - *Euaspis abdominalis*
  - *Chelostoma fuliginosum*
  - *Heriades carinatus*
  - *Osmia lignaria, subaustralis, subfasciata*
  - *Hoplitis albifrons* (Fig. 30; male, Fig. 31)
  - *Creightonella frontalis* (Fig. 32)
  - *Megachile albitarsis* (Fig. 33), *frugalis*
  - *Chalicodoma exilis* (Fig. 34)

FAMILY APIDAE
- Subfamily Meliponinae
  - *Meliponula bocandei* (Fig. 35)
  - *Trigona beccarii, braunsi, capitata* (Fig. 36), *chanchamayoensis, cupira, erythrea, mexicana*
  - *Dactylurina staudingeri*
  - *Lestrimelitta limao*
  - *Melipona fasciata*
- Subfamily Apinae
  - *Apis mellifera* (queen, Fig. 37; worker, Fig. 38)
- Subfamily Bombinae
  - *Euplusia violacea* (Fig. 39)
  - *Euglossa cordata*
  - *Eulaema dimidiata*
  - *Exaerete smaragdina* (Fig. 40)
  - *Bombus americanorum* (Fig. 41)
  - *Psithyrus variabilis* (Fig. 42)

section. Figure 1 illustrates certain structures not labeled in the remaining figures, but most ridges and grooves are labeled on all the figures where they appear. To avoid crowding the illustrations, structures along the upper and lower mandibular margins are minimally labeled. For example, in most of the illustrations the distal part of the adductor ridge, where it appears on the outer mandibular surface below the condylar groove, is not labeled. Structures on the upper mandibular margin such as the upper carina are ordinarily labeled on only one rather than both of the drawings of each mandible.

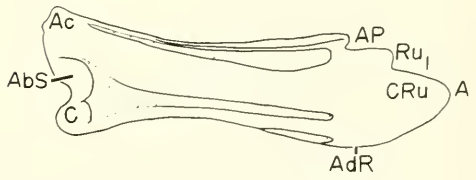


FIG. 1. Outer view of mandible of *Diphaglossa gayi*, female, with labels for structures not identified in other illustrations. For abbreviations see Tables 2 and 3.

Dots on the drawings indicate the areas with hairs. The meanings of the abbreviations are indicated in Tables 2 and 3.

Most of the terminology is new for this paper but (where practical) terms are those used by Michener (1944) and Eickwort (1969).

BASIC STRUCTURE AND TERMINOLOGY

For purposes of terminology, the mandible is considered to lie in a horizontal position (as when it is closed), so that it has upper and lower margins separating the inner and outer surfaces. Eickwort (1969) considered the mandible to project downward and to have anterior and posterior margins, but our assumptions seem more practical to us.

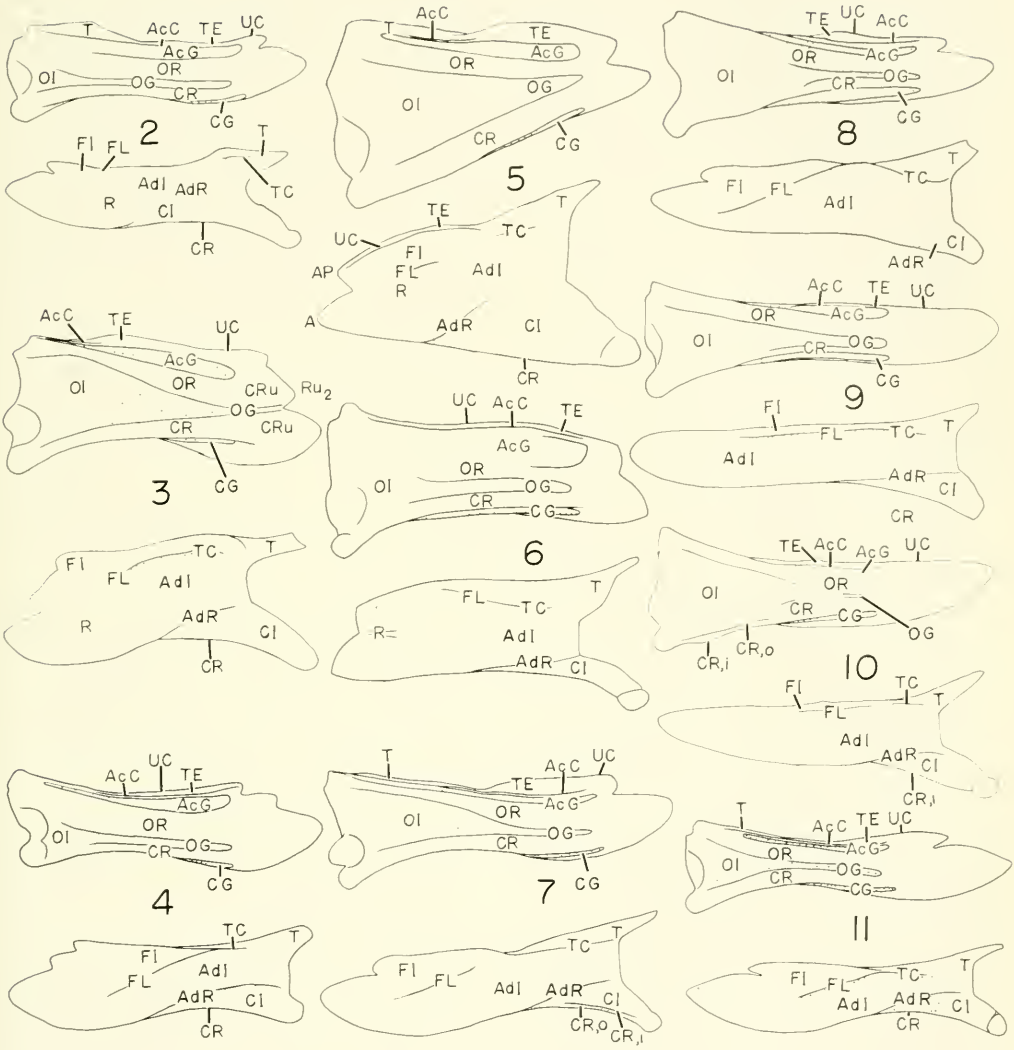
Mandibular Base: The base of the mandible is attached to the head capsule at the large and irregularly round mandibular socket between the lower end of the eye and the proboscidial fossa. In this socket the mandible can rock only in one plane, because of the double articulation consisting of the small anterior *mandibular acetabulum* (Ac), fitting over a condyle near the lower lateral angle of the clypeus, and a large posterior *mandibular condyle* (C), fitting into an acetabulum in the cranium below the eye. The line between these two articulations is the *articular axis,* about which the mandible rocks.

The outer margin of the mandibular socket is only moderately deviant from the articular axis. A small bulge in the outer margin of the mandibular base, a short distance in front of the mandibular condyle, is the *abductor swelling* (AbS) to which the *apodeme of the abductor muscle* is attached. Opening of the mandibles requires little power and the abductor swelling, as might be expected, is not far lateral to the articular axis; it provides no great mechanical advantage.

The main work of mandibles, i.e., biting, excavating soil or wood, and the like, requires strength in closing the mandibles. The inner margin of the mandibular socket is accordingly far mesal to the articular axis and the inner margin of the mandibular base is swollen to form the *adductor convexity,* sometimes called the adductor angle. To this convexity, far mesad from the articular axis and providing considerable mechanical advantage, is attached the *apodeme of the adductor muscle.* The whole inner basal mandibular surface is involved in the adductor convexity, while only a small local area forms the abductor swelling. The summit of the convexity is usually flattened and lies between the basal part of the adductor ridge and the trimmal carina (see below).

Mandibular Surfaces: If an imaginary "plane" through the articular axis were extended toward the mandibular apex, curving and sometimes twisting with the curvature of the mandible so that the maximum area of the plane is internal, i.e., inside the mandible, then the lines of intersection of the plane with the mandibular surface will separate the *outer surface* of the mandible from the *inner surface.* The outer surface is ordinarily gently convex, never far from this imaginary plane. The inner surface, commonly concave distally, is strongly convex basally, forming the adductor convexity. The lines along which the imaginary plane intersects the mandibular surface are the *lower margin* and the *upper margin* of the mandible. The details of the intersection of the plane with the mandibular surface vary, so that certain structures cannot be unhesitatingly attributed to one or the other surface.

The adductor convexity is often so large that, for the basal half of the mandible, the upper (or anterior) slope of the convexity could be considered as an upper (or anterior) mandibular surface, commonly beveled to pass the clypeal and labral margins when the mandibles are being



Figs. 2-11. Outer and inner views of mandibles of female Colletidae, Halictidae, Andrenidae, Oxaeidae, and Melittidae. For species names see Table 1; for abbreviations see Table 2 and 3.

closed. Likewise, for the basal part of the mandible, the lower or posterior slope of the adductor convexity could be regarded as a lower (or posterior) mandibular surface. Because upper and lower surfaces are not evident distally, it seems simplest not to use these terms, but to consider both as parts of the inner surface.

Outer Surface: Seen from the outer side, many bee mandibles have a preapical tooth (subapical tooth of Eickwort, 1969; Michener, 1944, etc.) on the upper margin; this tooth and the area basal to it are the pollex (thumb) while the remainder of the mandible is termed the rutellum (mitten). (For further details see below.) The outer

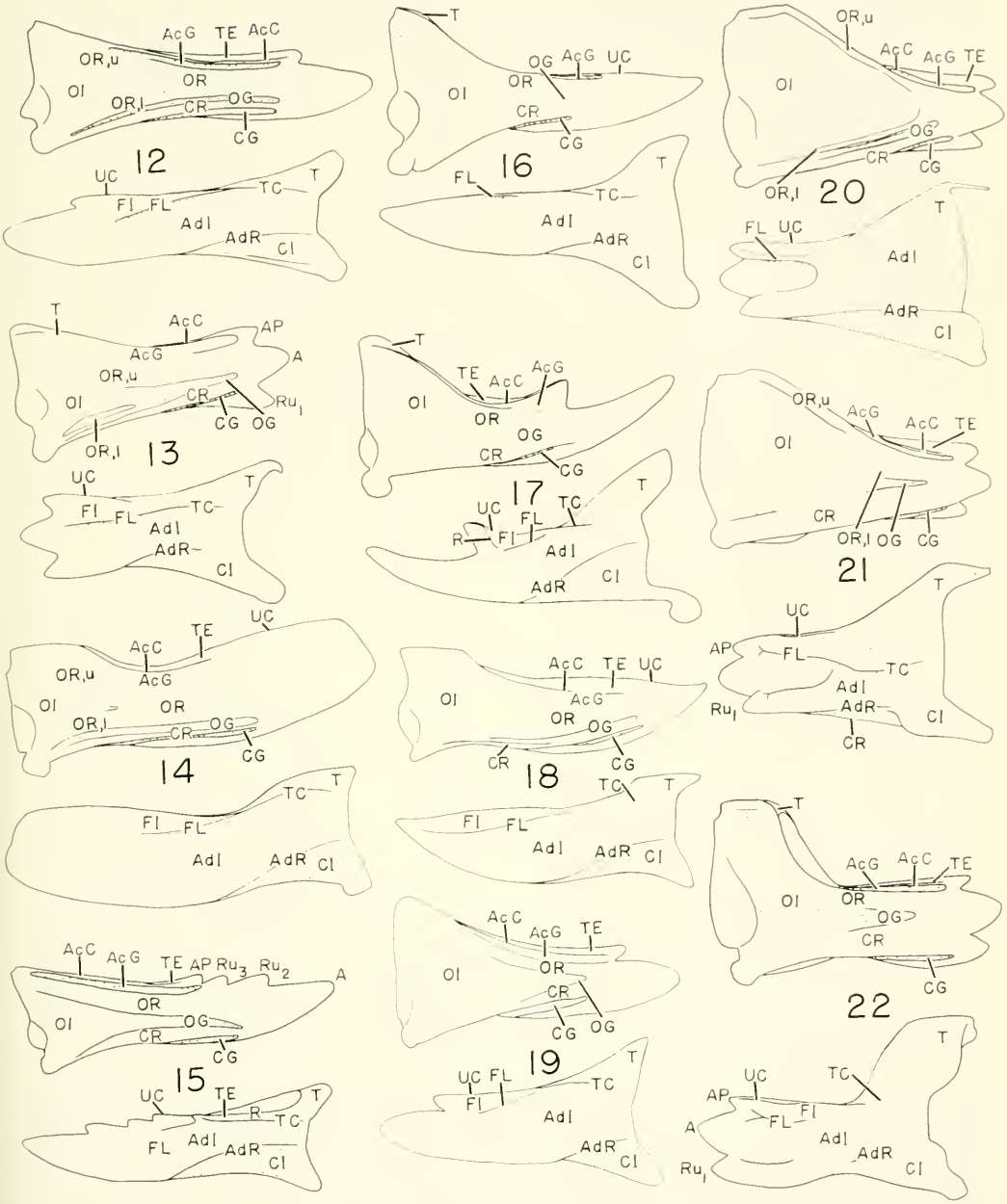
surface of the mandible usually has several longitudinal, elevated areas or ridges that are normally smooth and hairless. They fuse toward the apex of the mandible to form a smooth surface, the *cap of the rutellum* (CRu). Between the ridges are grooves, almost always bearing hairs. Commonly, one groove (outer) is broadened basally, forming a more or less flat, non-elevated, hairy area that cannot reasonably be called a groove and is therefore called an interspace. Another groove (acetabular) in some bees (especially Megachilidae) is broadened apically to form an interspace that often contains longitudinal ridges which are probably secondary, not homologous to any of the more universal or primary, named ridges.

The lower margin of the mandible basally and sometimes apically is formed by the *condylar ridge* (CR) which arises near the mandibular condyle and extends toward the apex of the mandible, ultimately joining the cap of the rutellum. Usually, however, in the distal half of the mandible, the adductor ridge from the inner surface of the mandible comes into view below the condylar ridge, so that the lower margin of the mandible is formed distally by the adductor ridge, which also merges with the cap of the rutellum apically. Occasionally, as in *Halictus quadricinctus* and *Bombus,* the condylar ridge consists of two (even three) ridges with a hairy groove between them; one is clearly on the outer mandibular surface (CR, o) while the other is often on the lower margin or almost onto the inner surface (CR, i).

Above the condylar ridge and typically parallel to it is the piliferous *outer groove* (OG) which usually expands basally to form the broad, hairy *outer interspace* (OI) (but see below). Rarely, as in *Euplusia,* the distal part of the outer groove is divided, forming an upper and lower outer groove (OG, u; OG, l). Alternatively, elevation of all but marginal areas of the outer interspace may divide the median and basal parts to form upper and lower outer grooves, as in *Bombus* and *Psithyrus.*

Above the outer groove is the commonly broad and gently convex *outer ridge* (OR) (outer diagonal ridge of Eickwort, 1969) which distally is separated by the outer groove from the condylar ridge, and which merges distally into the cap of the rutellum. The outer ridge commonly occupies the median part of the outer surface of the mandible. Basally, the outer ridge usually curves upward (hence Eickwort's term, diagonal ridge) so that when complete, its base is near the acetabulum. When there is more than one base, this one is termed the upper root (OR, u). Sometimes, as in *Diphaglossa,* the upper root of the outer ridge is broad, so that its base occupies the space between the acetabulum and the abductor swelling; alternatively, the outer ridge may fade away basally into the outer interspace, the base of the upper root being represented, if at all, by an elevation just distad from the acetabulum and not connected to the distal part of the ridge. Other roots of the outer ridge are relatively rarely developed. Sometimes the ridge has a lower basal ramus or root (OR, l) extending toward the condyle (e.g., *Macrogalea, Anthophora*) or a median root (OR, m) extending toward the abductor swelling (e.g., *Chalicodoma*). In these cases, which are very similar to one another and probably represent the same development, the outer interspace lies between the two roots of the outer ridge. The outer ridge is so named because of its position; its basal connections are variable and not appropriate for purposes of naming the ridge.

When the outer ridge has lower or median roots, the outer groove is narrow to the base of the mandible and cannot



FIGS. 12-22. Outer and inner views of mandibles of female Anthophorinae, Nomadinae, and Xylocopinae in the Anthophoridae. For species names see Table 1; for abbreviations see Tables 2 and 3.

expand into the outer interspace. An alternative interpretation would be that such roots are really formed by duplication of the condylar ridge. Examination of mandibles like those of *Anthophora* or *Clisodon,* however, show that the apex of the outer groove is in the same position as in most bees, and the extra ridge arises from

the preapical part of the outer ridge. Mandibles like those of *Allodape* and *Xylocopa* show intermediate stages in development of lower roots.

Rarely, the distal part of the outer ridge may be deeply bifid, forming upper and lower branches (OR, d; OR, v) as in *Bombus*.

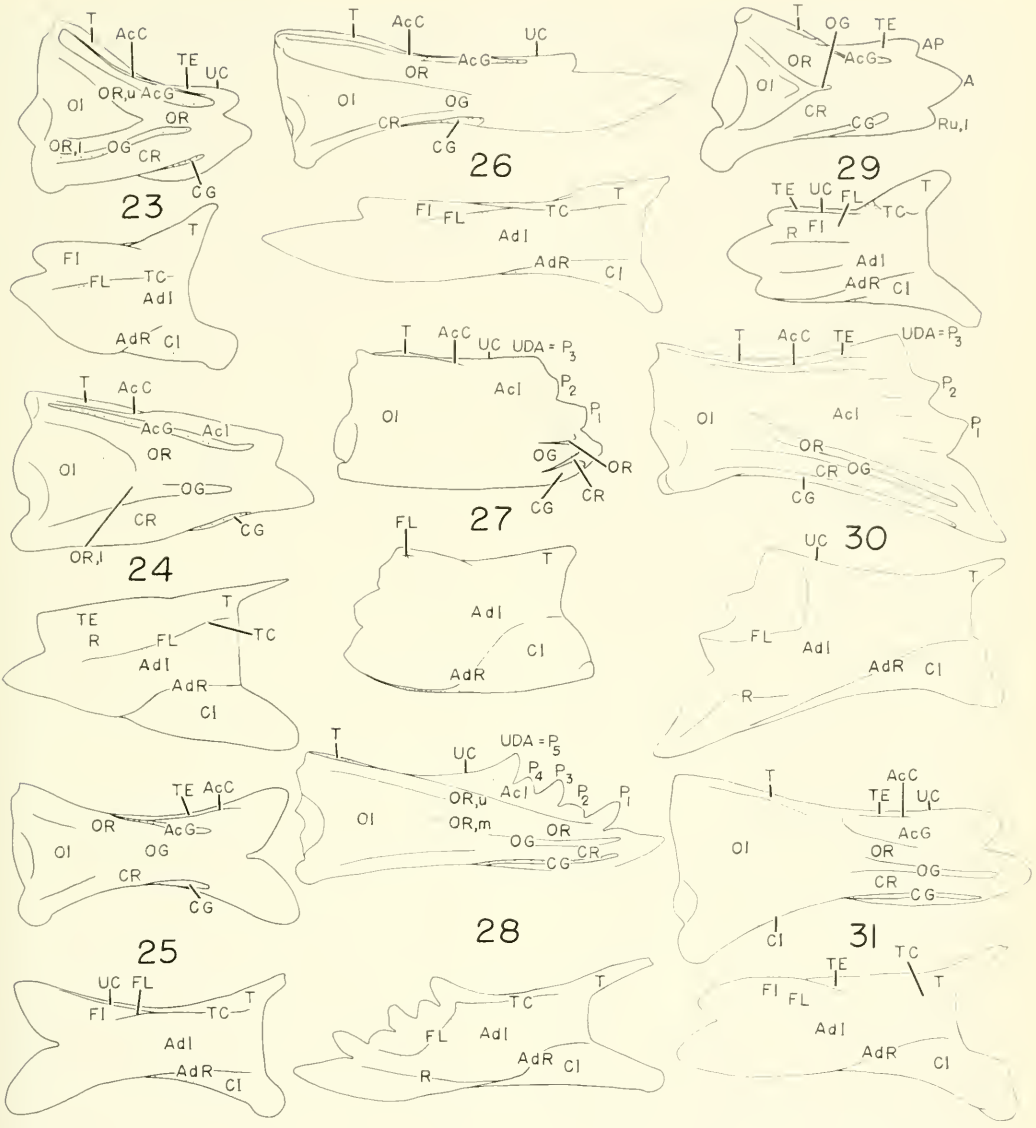
Above the outer ridge is the piliferous *acetabular groove* (AcG) (outer anterior groove of Eickwort, 1969), which arises distal to the acetabulum and extends toward the distal margin of the mandible. It usually fades away near the base so that the outer ridge (or its upper root) fuses with the acetabular carina basally. It ordinarily terminates before the distal margin of the mandible, and more or less separates the *pollex*, which usually forms the upper preapical mandibular tooth or margin, from the rest of the mandible (as seen from the outer surface), the *rutellum*. Thus, it does not end in the cap of the rutellum as do the grooves below it on the outer surface. [The rutellum and pollex are not separable on the inner, mandibular surface except by the notch on the distal margin in most species. Eickwort (1969) believed that the fimbriate line separates the pollex from the rutellum (our terminology) on the inner surface of the mandible, but this is ordinarily not the position of the fimbriate line.] Above the acetabular groove is the *acetabular carina* (AcC), a usually sharp ridge which arises near the acetabulum and extends distally toward the apex of the pollex. On the basal part of the mandible, the acetabular carina and the outer ridge are sometimes completely fused. This appears to be the case, for example, in male *Hoplitis* and in *Megachile* and *Chalicodoma*.

In some bees (Megachilidae, Apidae) the distal part of the mandible, above the outer ridge, is expanded apically as a broad space between the distal parts of the outer ridge and the acetabular carina. This space constitutes, or is occupied by, the acetabular groove in slender mandibles, but that term is inappropriate for a broad space, especially when there are several secondary ridges or possibly branches of the outer ridge in the area. This area is therefore called the *acetabular interspace* (AcI).

The acetabular carina may be the upper margin of the mandible. If not, the space and carina commonly narrowly visible above the acetabular carina have their principal connections with the inner mandibular surface and are described in the next section.

In some megachilid bees a striking feature is the *outer premarginal fimbria*, which arises from the *outer premarginal impressed line* (OIL). The fimbria or line roughly parallels the distal margin of the mandible across the acetabular interspace, but is absent in the region of the apex proper, i.e., on the cap of the rutellum. In the Meliponinae, there are no ridges on the outer mandibular surface or only the acetabular carina, but an *oblique groove* (OG) extends from near the acetabulum toward the mandibular apex. It seems likely that, near its base, the oblique groove is the acetabular groove, but distally it must be a secondary groove, for it goes toward the mandibular apex and has a branch going to the lower margin of the mandible. No such pattern occurs in the mandible of other bees.

Inner Surface: Arising on the adductor convexity is the *adductor ridge* (AdR). This ridge, the basal part of which is often not hairless and shining like ridges of the outer surface, follows a characteristic course, curving downward in the median part of the mandible toward the lower margin; thereafter it extends distally, commonly forming or being very near to the lower mandibular margin. This distal part of the adductor ridge was called the outer posterior ridge by Eickwort (1969). The



FIGS. 23-31. Outer and inner views of mandibles of female (except for Fig. 31) Xylocopinae in the Anthophoridae, Fideliidae, and Megachilidae. For species names see Table 1; for abbreviations see Tables 2 and 3.

interval above the adductor ridge distally on the outer surface of the mandible, separating it from the condylar ridge, is the *condylar groove* (CG) (outer posterior groove of Eickwort, 1969). Basally, this interval is on the inner surface of the mandible and, because of the curvature of the adductor ridge, the interval becomes the broad lower surface or slope of the adductor convexity, i.e., the *condylar interspace* (CI).

Above the adductor ridge on the inner mandibular surface is the rather broad *adductor interspace* (AdI). This interspace is the median zone of the inner mandibular surface and is delimited above by the fimbriate line and trimmal carina.

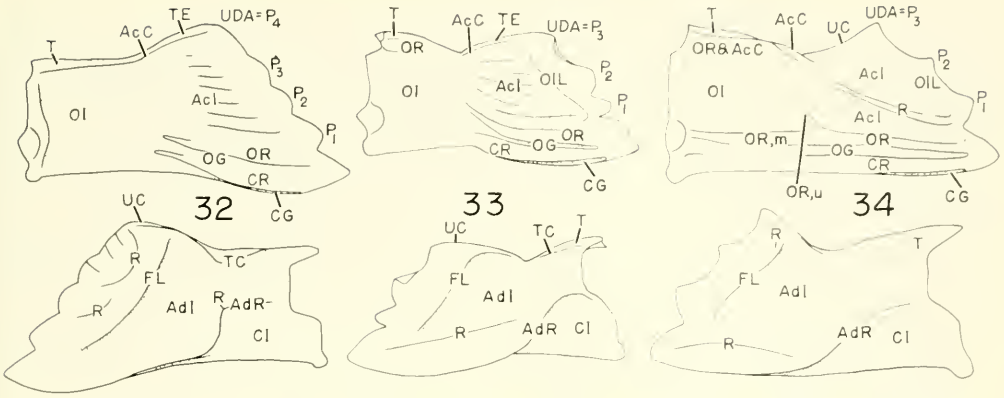
The *trimmal carina* (TC), sometimes

merely a ridge basally, arises on the upper surface of the adductor convexity and separates the basal part of the adductor interspace from the often flat *trimma* (T), a special basal mandibular area which is usually smooth and often bears some short, presumably sensory hairs and which slopes toward the upper margin of the mandible and passes the clypeal and labral margins when the mandible is being closed. The trimma forms the upper surface or slope of the adductor convexity and extends to the acetabulum; toward the outer mandibular surface it is limited by the acetabular carina if the latter extends far enough basally; if not, it is limited by the upper edge of the basal root of the outer ridge, which is probably fused with the base of the acetabular carina. The trimmal carina commonly extends distally to about the middle of the mandible. From there, it sometimes continues uninterruptedly as the *upper carina* (UC) of the distal part of the mandible, which usually forms the upper margin of the pollex. The interval between the acetabular carina and trimmal and upper carinae, basally the broad trimma, tapers distally to form a slender *trimmal extension* (TE) on the pollex. This is not a piliferous groove but a smooth area, as is the trimma.

Sometimes merging with the distal end of the trimmal carina and curving distally, often obliquely across the inner surface of the mandible, is the *fimbriate line* (FL). This is the line on which the often elevated upper part meets the often depressed median part of the inner mandibular surface. Sometimes the line is a ridge or a carina (the *fimbrial carina*), more often simply a step between two levels. The fimbriate line is usually marked by a series of hairs along its lower margin, hence its name; these hairs constitute the *inner fimbria*. The space between the fimbriate line and the upper carina is the *fimbrial interspace* (FI). It disappears basally where the upper carina and fimbrial ridge approach one another or unite, but distally it may expand to form the whole upper distal part of the concave inner surface of the mandible. In those bees (especially the Megachilidae) in which the mandibles are broad distally due to the expansion of the condylar interspace on the outer surface, an effect on the inner surface is that the fimbriate line becomes very oblique, even parallel to the distal margin of the mandible. The point where it fuses with or approaches the upper or trimmal carinae moves distad, often quite close to the upper distal angle of the mandible, thus essentially eliminating the fimbrial interspace.

The inner fimbria sometimes arises from a weak groove, called the inner anterior groove by Eickwort (1969), but it is ordinarily depressed only relative to the space above it and not relative to the space below it. Hence we have not used the word groove for it. When the fimbriate line is carinate, the carina may overlap the bases of the fimbrial hairs, which therefore emerge from behind the carina.

Relations among the trimmal carina, the upper carina, and the fimbriate line vary. Sometimes the three do not meet. Sometimes all three meet, forming a single Y-shaped system. Sometimes the trimmal carina continues uninterruptedly as the upper carina, with no connection to the fimbriate line. Sometimes the trimmal carina continues uninterruptedly as the fimbriate line without connection with the upper carina. Under these circumstances, there seems to be no alternative to three separate terms for the three structures. It may be, however, that the trimmal carina and fimbriate line constitute a single basic structure, sometimes interrupted medially, to which the upper carina is sometimes joined. This suggestion is based on the fact that the trimmal carina, like the fim-



Figs. 32-34. Outer and inner views of mandibles of female Megachilidae. For species names see Table 1; for abbreviations see Tables 2 and 3.

briate line, typically has a row of hairs along its lower margin. In fact, when the carina is weak or absent, its location is sometimes indicated by the row of hairs; the same is sometimes true of the fimbriate line.

Distal Margin: The distal or apical margin of the mandible varies from a single, narrowly rounded or pointed tip to a long, simple to multidentate edge. The *apex* (A), the distal extremity of the cap of the rutellum, is the part of the mandible farthest from the base and except in most Lithurginae and Xylocopinae and in *Clisodon* in the Anthophorinae, it forms the tooth that is a continuation of the lower margin of the mandible, often called the first tooth and here recognized as the first tooth of the rutellum. In some bees (e.g., *Panurginus*) there are no teeth, i.e., the mandible is simple and toothless.

In many bees there is a preapical tooth, the *apex of the pollex* (AP), on the upper margin. In such cases the mandible is often called bidentate, and the apex and preapical tooth constitute the distal margin.

In some bees such as *Centris,* the distal margin of the rutellum above the apex and below the pollex bears one to several teeth, the *upper teeth of the rutellum* (Ru_2, Ru_3, etc., Ru_1 being the apex). In some (most Lithurginae and Xylocopinae and *Clisodon*), there is a rutellar tooth below the apex and formed from the end of the adductor ridge. This is the *lower tooth of the rutellum* (Ru, l). When it is present, the distal margin of the mandible is tridentate, with the median tooth (mandibular apex) longest and with the lower tooth of the rutellum below it and the similarly shaped apex of the pollex above it.

In most female Megachilinae and to a lesser degree in some aphids, the distal margin of the mandible is elongate, because the region of the pollex is expanded distally to form two to several *teeth of the pollex* (P_1, P_2, etc.) or an edentate margin. The upper end of this margin or the uppermost tooth is the *upper distal angle* (UDA) or simply the upper angle (inner angle of much taxonomic work; we have avoided this term because it is not on the inner surface of the mandible).

Summary and Abbreviations: To summarize and organize the terminology, the longitudinal ridges, grooves, and interspaces are listed in Table 2, starting with the condylar ridge and proceeding upward on the outer surface of the mandible and continuing around the upper margin and downward on the inner surface. Distal structures that are, or may be, continuations of basal structures are indented below the name of the basal structure. In-

TABLE 2

RIDGES, GROOVES AND INTERSPACES.

condylar ridge	CR
(when compound or additional ridges, outer and inner)	o, i
outer interspace	OI
outer groove	OG
(when compound, upper and lower)	u, l
outer ridge	OR
(upper median, and lower roots of outer ridge)	u, m, l
(upper and lower distal branches)	d, v
acetabular groove	AcG
acetabular interspace	AcI
acetabular carina	AcC
trimma	T
trimmal extension	TE
trimmal carina	TC
fimbriate line	FL
upper carina	UC
fimbrial interspace	FI
adductor interspace	AdI
adductor ridge	AdR
condylar interspace	CI
condylar groove	CG

TABLE 3

OTHER MANDIBULAR STRUCTURES.

mandibular acetabulum	Ac
mandibular condyle	C
abductor swelling	AbS
apex (=1st tooth of rutellum)	A
upper teeth of rutellum	Ru_2, Ru_3, etc.
lower tooth of rutellum	Ru, 1
cap of rutellum	CRu
teeth of pollex	P_1, P_2, etc.
apex of pollex (commonly preapical tooth)	AP
unnamed "secondary" ridges in certain genera or species	R
outer premarginal impressed line (Megachilidae)	OIL
upper distal angle (Megachilidae, Apidae)	UDA
oblique groove (Meliponinae)	og

dented items in parentheses are subdivisions of major structure.

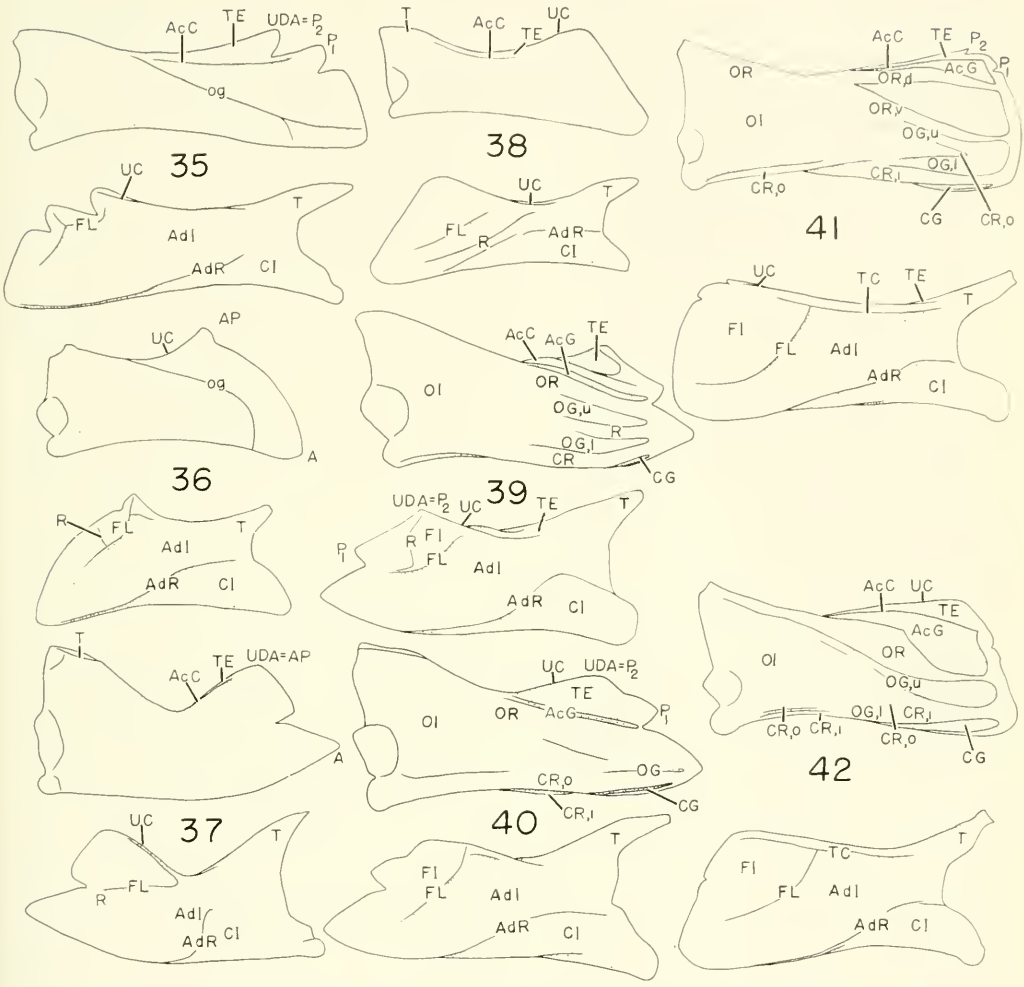
Other special terms used are italicized in the preceding account. Those whose abbreviations are used in the illustrations are listed in Table 3.

COMPARATIVE STUDY

The Ancestral Type of Mandible: In a large group of ground-nesting bees, the mandibles are rather slender, usually with all or most of the structures listed in the preceding section in readily recognized form. Such mandibles occur in the Colletinae (Figs. 2, 3), Diphaglossinae (Fig. 1), Stenotritinae, Halictidae (Fig. 7), Andrenidae (Fig. 8), Oxaeidae (Fig. 10), Melittidae (Fig. 11), Anthophorinae (Fig. 12) and Fideliidae (Fig. 26).

Mandibles of this type occur also among sphecoid wasps. For this reason we consider them as ancestral among bees. Considerable variation occurs, however, among such mandibles. Some unusual and presumably derived features of certain mandibles in this group of bees are described below.

Colletid groups such as the Paracolletini (*Leioproctus* spp.), Diphaglossinae and Stenotritinae have rather ordinary mandibles. In *Colletes* (Fig. 2) and *Ptiloglossa* the adductor ridge fades out medially so that the basal part, on the adductor convexity and distal to it, is not clearly connected to the distal part along the lower margin of the distal half of the mandible. A continuation of the basal part extends distally, however, toward the mandibular apex, as a broad, secondary, longitudinal median ridge in the adductor interspace, a special and doubtless derived ridge not found in most other bees. A similar secondary ridge is weakly developed in *Callomelitta*. The latter genus is unusual for having the rutellum divided to form two teeth, a modification possibly associated with nesting in wood instead of soil.



Figs. 35-42. Outer and inner views of mandibles of female Apidae. For species names see Table 1; for abbreviations see Tables 2 and 3.

Halictids show only limited diversity in mandibular structure. In *Halictus quadricinctus,* but not in related bees such as *H. ligatus* and *Lasioglossum,* an inner condylar ridge lies just beneath the basal part of the lower mandibular margin and extends from near the condyle to the marginal part of the adductor ridge, leaving a pilose groove just behind the usual (outer) condylar ridge. Some wood-nesting halictids have slightly modified mandibles. Thus, *Augochlora pura* has the trimmal extension irregularly shaped and *Megalopta genalis* has the same feature and in addition two large teeth on the inner mandibular surface. These seem to be enlargements of the fimbrial carina, since there are a few hairs, more or less in line with those along the trimmal carina, above each of the teeth. In the Nomiinae (*Nomia*) and Dufoureinae (*Dufourea, Systropha*), the mandibles are ordinary and the fimbriate ridge is a mere change in level (depressed below the line), with no hairs in *Systropha.*

Andrena accepta and, to varying degrees, other species of *Andrena* are unusual in having the adductor ridge directed downward almost from its base so that the condylar interspace is very short and the condylar groove correspondingly long.

In the Panurginae such as *Panurginus*, *Panurgus*, *Perdita*, and *Psaenythia*, the pollex is reduced and does not form a tooth. *Psaenythia* has a longitudinal, median secondary ridge in the adductor interspace suggestive of that of *Colletes*, but it is not connected with the adductor ridge and is presumably of independent origin.

Protoxaea (Oxaeidae) has an inner condylar ridge similar to that of *Halictus quadricinctus*. It may be a feature of large, slender mandibles. Other striking features of the mandible of *Protoxaea* are lack of the tooth at the apex of the pollex and the weak condylar and outer ridges that are adjacent to one another distally before merging with the cap of the rutellum.

All four subfamilies of Melittidae have quite ordinary mandibles. The most unusual is *Dasypoda*, in which the mandible is unusually strongly curved and the cap of the rutellum is enormous, almost half as long as the mandible, as a result of the short grooves on the outer surface.

The Fideliidae also falls in the group showing ancestral mandibular structure. In *Fidelia* the tooth of the pollex is enormous, as large as the rutellum. In both *Fidelia* and *Neofidelia* the trimmal carina, upper carina, and the brief fimbriate line unite in a Y-shaped pattern.

In the nest-making Anthophorinae (examined in *Anthophora*, *Svastra*, *Melissodes*, *Centris*, *Diadasia*, *Melitoma*, *Exomalopsis*, *Tapinotaspis*, etc.), the mandibles are of the common ancestral type, with deviations in certain genera as mentioned in subsequent paragraphs.

The relations of the trimmal carina, upper carina, and fimbriate line vary widely even among bees having the generally ancestral mandibular type. In some (e.g., *Colletes*), all three structures are separated. In *Diphaglossa*, *Fidelia*, *Neofidelia*, *Svastra*, and some *Anthophora*, all are connected to form a Y-shaped complex and this is nearly true, also, in *Melitta* and *Andrena*. In bees such as *Anthophora*, *Panurginus*, and *Protoxaea*, the hairs just below the fimbriate line and trimmal carina form a single continuous row and the point where the trimmal carina stops and the fimbriate line begins is quite arbitrary. This is almost true of *Centris*, also. In *Halictus* the trimmal and upper carinae are united with one another and isolated from the fimbriate ridge. In the panurgines and *Protoxaea*, the fimbriate line is even more longitudinal than in most of the bees here discussed, a common feature among bees with slender mandibles. In *Protoxaea* the upper carina extends farther basad than usual, parallel to and almost as far as the trimmal carina. A short transverse ridge extends from the fimbriate line to a weak elevation of the upper carina.

The outer ridge in mandibles of the general ancestral type ordinarily is rather uniformly wide basally and curves upward to the vicinity of the acetabulum. In *Diphaglossa*, it is much widened basally, more than half as wide as the mandible, and almost replaces the outer interspace. In *Svastra*, *Anthophora* and in *Ctenocolletes*, the outer ridge has two bases, the usual upper root near the acetabulum and another, the lower root, directed toward the condyle. The lower root separates the outer groove from the outer interspace; the outer groove continues nearly to the base of the mandible and the interspace lies between the two roots of the outer ridge.

Parasitic anthophorids: Mandibles of the Nomadinae, as well as of the Melectini and Ctenioschelini of the Anthophorinae, i.e., of the parasitic Anthophoridae, are also

similar to those of the ancestral type but shorter, more like those of many males. Basal parts of the condylar and outer ridges in these parasitic forms fade into the outer interspace, not reaching the base of the mandible or in *Thyreus* reaching the base, but weakly differentiated. In *Nomada* and *Ericrocis* the tooth of the pollex is absent; it is unusually large in *Thyreus* and *Melecta*. The acetabular carina is absent in *Ericrocis* and the acetabular groove is represented only by a short row of hairs in an area that is otherwise a continuum from the outer ridge to the upper carina. In *Thyreus, Melecta,* and *Ericrocis,* the trimmal carina seems continuous with the upper carina; the fimbriate line is absent but the fimbria is present, slanting away from the upper carina and in the melectines continuous with the hairs along the trimmal carina. Such mandibles are variably simplified as compared to the ancestral type; those of *Biastes* (Fig 19) are the least simplified of any parasitic anthophorid studied and would easily be placed among the mandibles of the ancestral type discussed in the preceding section.

Hylaeinae and Xeromelissinae: Other somewhat modified mandibles include those of the colletids that use preformed burrows or excavate pith, the Hylaeinae and Xeromelissinae. *Amphylaeus,* for example, has short mandibles, broad at the base and tapering apically (Fig. 5), with the cap of the rutellum much reduced by the outer interspace—outer groove which together form a broad triangle. The acetabular groove is broad, the acetabular carina absent as a sharp ridge, there being no carina, but only a space or "ridge" between the acetabular groove and the trimmal extension. The upper carina is on the inner surface of the mandible. A strong, broad secondary ridge, suggestive of that of *Colletes,* extends from the basal portion of the adductor ridge across the adductor interspace toward the distal part of the mandible. In *Hylaeus* this ridge is absent. Moreover, the trimmal carina and fimbriate line are absent; there is only a rounded surface separating the trimma from the adductor interspace. Also in *Hylaeus* the upper carina is in its usual position on the upper margin of the pollex.

Chilicola has more elongate mandibles.

An unusual feature is the extraordinarily broad acetabular groove.

Xylocopinae and Lithurginae: Bees of these subfamilies, separated according to usual classifications into two, well known families, the Anthophoridae and Megachilidae, have short mandibles, wide at the bases and commonly tridentate at the apices, because of the lower tooth of the rutellum which is the enlarged apex of the adductor ridge, in addition to the usual upper preapical tooth which is the apex of the pollex. [*Anthophora* (or *Clisodon*) *terminalis* has similar mandibular dentition although the mandible is more elongate.]

Macrogalea, Allodape, and *Ceratina* have the outer ridge narrow and at the upper margin of the large outer interspace; the ridge is carinate in *Macrogalea.* In *Macrogalea* there is a lower root of the outer ridge, a feature present also in *Manuelia.* In *Manuelia, Xylocopa,* and *Lithurge,* the outer and condylar ridges are both broad, so that the outer interspace is small. The mandibles of all these bees tend to have a deep, longitudinal depression in the middle of the apical half of the inner surface. The fimbriate line in the Xylocopinae, if recognizable, is longitudinal and along the upper margin of this depression, but in *Lithurge* it is oblique and well above the depressed area.

The ground-nesting genus *Proxylocopa* has more slender mandibles than most *Xylocopinae,* without the lower tooth of the rutellum, thus resembling the basic ancestral mandibular type. Many wood in-

habiting species of *Xylocopa,* however, also lack this tooth, as shown for *X. virginica* (Fig. 24).

Megachilinae: The megachilines are remarkable for the tendency of the mandible to be broad, with the apex multidentate, especially in females. This breadth is achieved by great broadening of the area of the acetabular groove (i.e., the space between the outer ridge and the acetabular carina) to form an acetabular interspace, itself often with multiple, secondary, longitudinal ridges or rami of the outer ridge. This development, which is also seen to a lesser degree in the Apidae, is interpretable on the basis of females alone but verified from examination of males (Fig. 31), which have more slender mandibles. The acetabular groove is not particularly wide in male *Hoplitis,* for example, and the identity of the condylar and outer ridges seems clear.

The variation in the outer ridge makes one question its homology when examining species of certain other genera, especially the females. The two ridges that terminate, as in all bees that have such ridges, on the apical or first mandibular tooth (cap of the rutellum) must be the condylar and outer ridges. It is the more basal parts of the latter ridge that sometimes become confusing. In the species illustrated, the outer ridge is not complete, but it is strong and continuous in forms such as *Osmia subaustralis, subfasciata,* and *lignaria,* which have mandibles otherwise similar to those of *Hoplitis.* The basal part of the other ridge is united with the acetabular carina in all these forms. In *Noteriades* sp., however, the outer ridge has two continuous roots, the usual upper one directed toward the acetabulum and uniting with the base of the acetabular carina, and another, the median root, directed toward the abductor swelling. In *Chalicodoma exilis* and *Chelostoma fuliginosum* the upper root is broken or entirely absent, but the median root is continuous, so that the ridge runs from near the abductor swelling toward the apex of the mandible. In these forms, a secondary ridge, comparable to a similar secondary ridge in *Anthidium,* extends from near the acetabulum (where it is probably the base of the upper root of the outer ridge and is united with the acetabular carina) across the acetabular interspace toward the distal margin near the apex of the mandible. Thus there are three ridges on the outer mandibular surface leading toward the apex of the mandible instead of two. (There seems to be no justification for regarding the upper of these three ridges as the acetabular carina and all the remaining upper toothed mandibular margin as an expansion of the trimmal extension; the latter, in most bees including related megachilids, is smooth and hairless, unlike the acetabular interspace.)

In *Heriades carinata* the distal part of the outer ridge has entirely lost its normal roots and, instead, is elevated and fused near the base with the condylar ridge. The mandible is thus left with a large area lacking ridges. An independent and far more extreme loss of ridges has occurred in *Anthidiellum,* in which the outer surface is hairy almost throughout, the hairy surface curving onto the condylar interspace without an intervening ridge. The distal parts of the grooves impinging on the small cap of the rutellum are broad, flat, and minutely hairy. The inner surface of the mandible is dominated by the broad, minutely hairy concavity of the distal part of the adductor interspace. All this is suggestive of features found in some Apidae and may be related to the fact that nests of *Anthidiellum* consist entirely of plastic material (resin), like the wax, resin, or mud utilized by Apidae.

The acetabular carina and trimmal extension are distinct in most megachilines,

but the carina is absent and the extension is therefore ill defined in *Anthidium* and *Callanthidium*. The trimmal carina is absent in female *Hoplitis,* but is usually present in megachilines, continuous with the fimbriate line or almost so, and both are margined on the lower side by a band or row of hairs. The fimbriate line is oblique or almost transverse, parallel to the distal margin of the mandible, in most female megachilids. In some forms, like *Hoplitis,* what appears to be the fimbriate line is angulate. In others, like *Creightonella,* there is a premarginal carina or line distal to the fimbriate line.

In *Creightonella* there is a short ridge branching from the adductor ridge and directed upward and distad. Another secondary ridge, likewise in the adductor interspace, is longitudinal and more nearly median in most megachilines.

In many megachilines (*Dianthidium, Paranthidium, Parevaspis, Euapis, Chalicodoma, Megachile frugalis* but not *albitarsis*), the distal part of the adductor ridge is provided with a strong fringe of erect hairs, as in the Meliponinae. In the same megachilines, the inner fimbria is often well developed, and in *Megachile frugalis* (not *albitarsis*) there is a conspicuous, outer premarginal fimbria.

Meliponinae and Apinae: These groups are remarkable for the lack of ridges and of the cap of the rutellum on the outer surface of the mandible. In Meliponinae a groove, perhaps in part the acetabular groove, is strongly evident. In *Apis* it is absent. When present, this oblique groove slants strongly across the mandible toward the apex (so that at least the distal part is presumably not the acetabular groove) and near the apex it branches, the lower branch going to the lower margin of the mandible, the upper continuing toward the apex. In *Meliponula* and some *Trigona* the acetabular carina is present, although weak. Except for the acetabular carina and the oblique groove (when they are present), the outer surface of the mandible is convex and rather uniformly hairy. The inner mandibular surface has a well formed adductor ridge. Distally this ridge is conspicuously fringed or hairy as in some megachilids and curves downward to form the lower margin of the mandible, but there is no condylar groove separating this margin from the rest of the outer surface of the mandible. The condylar interspace also is continuous with the outer surface of the mandible, with no intervening ridge. In workers, but not queens, of *Apis* there is a secondary, oblique carina in the adductor interspace, more or less parallel to the distal half of the adductor ridge. Such a carina is absent in Meliponinae. The fimbriate line is well developed in queens of *Apis,* less conspicuous in workers. In Meliponinae it is probably present, but its upper end is deflected distally toward the upper distal angle of the mandible. The trimmal carina is absent; the upper carina is present, forming the upper margin of the mandible distally, but does not approach the base of the mandible.

Bombinae: These large bees (see Figs. 39-42) have much more structure on the outer side of the mandible than do the Meliponini and Apinae. Thus in the Euglossini (*Eulaema, Euplusia*) there is a condylar ridge (double at the base or with an inner ridge behind the outer one as in *Halictus quadricinctus*) and an outer ridge (weak medially) delimiting an outer interspace and outer groove. Probably the distal half of the outer groove is double, with an upper and a lower branch, for an extra ridge branching from the median part of the outer ridge joins the upper part of the cap of the rutellum. Between the two branches of the outer groove is a secondary intercallary ridge. The acetabular groove is broad with a considerable space between the bottom of

the groove and the acetabular carina. The acetabular carina is strong and the trimmal extension is broad and with a minutely pubescent area apically. On the inner surface, the adductor ridge is normal, the trimmal carina is absent, but the acetabular carina reaches almost to the mandibular base; it is arcuate inward subbasally and then ascends toward the acetabulum. The upper carina is present, isolated from the oblique fimbriate line. Distal to the latter is an angular transverse premarginal ridge.

In *Euglossa* the mandibles are similar to those of *Euplusia,* but the ridges and grooves on the outer surface are weak except for the acetabular groove. *Exaerete* is also similar, but the outer ridge is only incompletely divided apically by depressed islands; none of the grooves ending on the outer surface of the rutellum contain finely pubescent distal areas, as in the nonparasitic genera.

In the Bombini the condylar ridge is compound, not only basally [where the uppermost ridge of the condylar ridge system was called the basal keel by Yarrow (1954)], but also on the apical part of the mandible where the lower or inner ramus is near the lower mandibular margin, the upper well above it, terminating on the outer groove in *Psithyrus* and as a process into that groove in *Bombus.* The distal part of that groove and of the grooves above it on the outer mandibular surface (also of the condylar groove, especially in *Psithyrus*) are broad, flat, nearly reaching the distal mandibular margin, and are covered with minute pubescence. As in *Euplusia* and most other Euglossini, the outer ridge is divided distally in *Bombus,* the upper ramus (Yarrow's main keel) separating a broad, intercallary depression or groove from the broad distal part of the acetabular groove. The lower ramus is Yarrow's second keel. All the "grooves" in Bombini are so broad and flat distally as to be better described as depressed areas, and the cap of the rutellum is a mere band on the distal margin of the mandible.

DISCUSSIONS AND CONCLUSIONS

Recognition of homologous features among the ridges and grooves of mandibular surfaces is possible and these features appear to shed light on relationships among bees. A common or "basic" pattern is found in mandibles of ground-nesting groups of bees of the families Colletidae, Halictidae, Andrenidae, Oxaeidae, Melittidae, Anthophoridae, and Fideliidae. These are, for the most part, bees that make their own burrows and cells in the soil. The same pattern is widespread among sphecoid wasps and it is presumably the primitive pattern for bee mandibles. Members of these groups that nest in wood (e.g., *Callomelitta* in the Colletidae; *Megalopta, Augochlora* s. str., and *Lasioglossum* (*Dialictus*) *caeruleum* in the Halictidae; and *Clisodon,* a close relative of *Anthophora,* in the Anthophoridae) have similar mandibles, often modified by the acquisition of extra teeth, or not recognizably modified as in the *Lasioglossum.* Most male bees have mandibles somewhat smaller and more slender than those of females, and often with certain ridges weak or absent. Parasitic Anthophoridae (Nomadinae, Melectini, Ctenioschelini) have somewhat simplified mandibles, suggesting those of many male bees (parasitic halictids do not show this tendency).

The groups of bees listed above occupy the whole base as well as some of the top of the phylogenetic tree for the bees as presented by Michener (1944), or in modified form by Michener (1974). There are various derived types of mandibles, however, as discussed below. Thus the colletid subfamilies (Hylaeinae and Xeromelissinae) that nest in preformed cavities in the soil, wood, or stems, or perhaps excavate in pith, have rather different man-

dibles. Such derived mandibular types are not found, however, among bees that make subterranean burrows and earthen cells.

A significant finding is the position of the Fideliidae clearly within the basic group. There is no doubt of the similarities of fideliid larvae to those of the Megachilidae (Rozen, 1973), a relationship supported by the metasomal scopa, but the mandibular structure, independent volsellae, wing venation, and other characters make us hesitant to place the Fideliidae in the Megachilidae.

The presence of a lower tooth of the rutellum and of a deep depression on the inner mandibular surface are similarities of the anthophorid subfamily Xylocopinae (most species) and the megachilid subfamily Lithurginae. Perhaps these similarities are convergences, as suggested by the different relation of the fimbriate line to the depression in the two groups, nearly all members of which burrow in wood or pith. Other characters will have to be analyzed before the meaning of this similarity is clear. The similar dentition of *Clisodon,* a wood inhabiting genus of an otherwise ground dwelling group, shows that at least this feature can appear by convergence and may indicate little about lines of descent.

Of much interest is the finding that in the Megachilinae and to a lesser extent in the Apidae, unlike other bees, the distal part of the condylar groove or the area immediately above it is expanded to form a condylar interspace. The toothed apical margins of mandibles of these bees are therefore largely derived from the pollex of ancestral groups. It is interesting that these are the two groups which commonly carry foreign materials to the nest for construction purposes. The megachilids generally have strongly toothed mandibles for cutting, preparing, and sometimes carrying materials such as leaves, plant hairs, pebbles, and resin. The apids have weak teeth (or lack them) and more scoop shaped mandibles for handling wax, resin, mud, and the like.

In the apid subfamilies Meliponinae and Apinae, the ridges and grooves on the outer mandibular surface are largely or almost wholly absent, the surface being convex and hairy. Loss of mandibular ridges and carinae may be convergent, associated with use of relatively soft materials (wax, resin, mud) in nest making, as suggested by the relatively featureless, hairy mandibles of *Anthidiellum,* a megachilid that makes nests of resin. Absence of ridges may also be associated with minute size, suggesting that the Meliponinae and Apinae arose from minute ancestors, a view supported for the Meliponinae by their reduced wing venation, a common feature of small insects.

The Bombinae have mandibular ridges. In the illustrations and discussion we have done our best to identify them with the ridges of other families of bees. However, secondary ridges are present (not the same in the Euglossini, *Psithyrus* and *Bombus*) and it is possible that most of the ridges arose newly in Bombinae from ancestors with few ridges like the Meliponinae. In Euglossini the grooves are reasonably similar to those of other families of bees although usually minutely pubescent apically. In the Bombini, however, the "grooves," at least apically, are broad, slightly depressed, flat areas covered with short, fine hairs.

The above remarks should not be used alone as a basis for reclassification of the Apoidea. However, they should not be ignored when such a work is done. The common derived characters of the Lithurginae and Xylocopinae, and of the Megachilinae and Apidae, may well result from convergence, but if they are supported by other findings, they will require restudy of the familial classification.

The functions of the ridges and grooves

are not known, but it is reasonable to assume that they serve to strengthen the mandibular cuticle. This view is supported by the tendency for weakened and sometimes also less numerous ridges and grooves in males and parasitic female bees, which do not make nests, and in bees that construct nests of soft materials like wax and resin.

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ECOLOGY AND EXPLOITATION OF *CTENOSAURA SIMILIS*

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ANNOUNCEMENT

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Ecology and Exploitation of *Ctenosaura similis*

Henry S. Fitch[1] and Robert W. Henderson[2]

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ABSTRACT

The giant herbivorous iguanid *Ctenosaura similis,* of southeastern Mexico and Central America, occurs in open woodland or edge habitat in seasonally dry lowlands. Sexual maturity is attained late in the second year, ovulation occurs about mid-February, and laying of the eggs (mean 43.4, 12-88) occurs about 5 weeks later. Hatchlings appear about mid-May and have tripled in length at the end of the first year when they are half-grown in length. Females outnumber males 2 to 1; but males are about 1.25 times female length and 1.8 times female weight. Biomass may be several kg per ha (1.67 per ha on a 10 ha sample area in Belize). Each ctenosaur centers its activity at a lookout and shelter; typical foraging radii are from 18.7 m in first-year young to 43.0 m in adult males. Food consists of many kinds of foliage, flowers and fruits, and some animal matter including small rodents, lizards, eggs, and insects. Exploitation of the ctenosaur is heavy in some parts of its range, including Nicaragua, where the species is a common article of diet for country people and also is sold by the hundreds in city markets. As a result, numbers have decreased drastically. Conservation is needed, especially protection of reproductive females, to assure a sustained yield of the flesh, a valuable natural resource.

INTRODUCTION

Ctenosaura similis, a giant iguanid lizard of southeastern Mexico and Central America, is of extraordinary interest eco-

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logically, being important in some areas as a game animal, as a source of high grade protein food for people and, at times, as a pest. Thus, and because it is an abundant and highly conspicuous member of the Middle American herpetofauna, we independently undertook ecological studies of it in Costa Rica and in Belize, respectively. Subsequently, we combined our efforts in a field study which centered in western Nicaragua and was encouraged and funded by the Banco Central of Managua, Nicaragua.

There, we investigated conservation oriented aspects of the ecology not included in our earlier studies, with attention to exploitation, past and present. Although further field work is desirable, the findings presented here will provide some basis for a general understanding of the ctenosaur's basic ecology, of its actual and potential value as a natural resource and of the measures necessary to preserve thriving populations with a sustained annual yield. We have here combined and integrated diverse data obtained from various localities over a 10-year period, for that purpose.

MATERIALS AND METHODS

In Costa Rica, from October 1967 to August 1971, intermittently, Fitch studied local populations at Quepos and Boca de Barranca, Puntarenas Province, and at Finca Taboga and Playas del Coco, Guanacaste Province, with casual observations elsewhere. The lizards, chiefly first-year young, were individually marked by toe-clipping. Measurements (S-V, tail) were recorded to the nearest millimeter and exact location was noted in each instance. Length was estimated for all those sighted from a car. At Belize City, in 1970-1971, Henderson (1973) also studied ctenosaurs by mark and recapture technique and observed the behavior and movements of recognizable individuals over periods of months. Our joint study in Nicaragua in February, March and April, 1976, involved examining ctenosaurs at city *mercados* (N= 827), and purchasing selected individuals (N=114) for examining gonads, and finding and interviewing professional hunters who supplied the city vendors. Those and others who hunted the lizards for home consumption provided information about ctenosaurs' population trends, local habits and the methods of securing them. Also, we collected series (N=160) for dissection and examination of stomach contents and gonads.

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ECOLOGY

Habitat: Over its extensive range, in Mexico east of the Isthmus of Tehauntepec, and Central America, *Ctenosaura similis* occurs in varied climates and plant formations, but it is absent from primary rain forest and from cool climates at high altitudes. One seen as a road kill, in June 1968, at Río Itiquis, Costa Rica Highway No. 1, Alajuela Province, approximately 900 m elevation was probably near the upper edge of the species' occurrence. The species is most prevalent on the relatively arid Pacific versant of Central America, but it intrudes onto the Caribbean versant and even reaches the Caribbean Coast and various small islands of the Continental Shelf in the western Caribbean.

The optimal habitat seems to be arid savanna. In Guanacaste Province, northwestern Costa Rica, and in Chinandega, León and Managua provinces, western Nicaragua, we observed high population densities in the dry season in areas made relatively barren by heavy grazing and/or annual burning of dead vegetation. Broken terrain with scattered, large trees, logs, loose boulders, rock outcrops, gullies with cutbanks, or streams with riparian thickets, provided the required shelter. Lava fields with a sparse vegetation are inhabited.

Ctenosaurs have often been found closely associated with cattle at corrals, salt blocks, and pasture edges. Such barren places provide the lizards with enough food from low weedy vegetation missed by the cattle and from foliage and flowers of trees.

Rock walls provide a superabundance of shelter and may have unusual concentrations of ctenosaurs. Fence posts, especially if large and hollow, are used both for basking and for shelter. Ctenosaurs often live on the margins of cultivated fields feeding on the crops and also on weeds.

The disturbed and seral conditions resulting from human activities often favor survival and increase of the ctenosaur, sometimes found living in close association with people. At the village of Playas del Coco in Guanacaste several were seen in a pig sty where they came to eat garbage. On the northern edge of Belize City and at Boca de Barranca, Puntarenas Province, Costa Rica, colonies of ctenosaurs lived among groups of buildings where vegetation was held in check by artificial trimming and by the trampling of large numbers of people (schoolyard, beach resort). Their burrows were beneath buildings. Many ctenosaurs were observed within the city of Managua, Nicaragua, in small, semi-isolated colonies in yards with trees and on roofs. Walled gardens provided an especially secure habitat. Other ctenosaurs lived in vacant lots with trees and grass, or lived among shacks or adjacent to warehouses or ruins where unused machinery, piled lumber, earthquake debris or trash provided shelter.

In the humid Caribbean lowlands, ctenosaurs are relatively scarce and localized in dry and open situations. On Great Corn Island, Zelaya Province, Caribbean Nicaragua, they were observed in forest and thick plantations, and appeared to be much more arboreal that their mainland counterparts. At Belize City, Neill and Allen (1959) found ctenosaurs in mangrove swamps, and Henderson (1973) found adults in the open areas about buildings, but found juveniles in a swampy and brushy adjacent area, often climbing in the bushes.

Burrows: Ctenosaurs dig effectively with alternate strokes of the powerful, clawed forefeet. Some find shelter above ground, in hollow limbs or fence posts, but most dig burrows where they are protected above by such objects as buildings, boulders, or tree roots. Vertical banks of road cuts or eroded gullies also provide favored sites and burrows often have well defined trails leading to them. The holes are flat bottomed, arched above, and wider than high, with winding and sometimes branched tunnels. Several that we excavated were between 1 and 2 m long. Some burrows have cavernous entrances, enlarged by digging predators or eroded by heavy rains. The tunnels are wide enough to permit the lizard to turn around inside and are horizontal or slope gently downward. Various snakes, lizards, rodents and arthropods use ctenosaur burrows for shelter.

Ctenosaurs do not emerge at night or on rainy days. Even when weather is favorable, the lizard does not emerge until well after sunshine has reached the burrow entrance. At first, only the head protrudes, and by gradual stages over perhaps half an hour, more of the body. Finally the lizard scrambles to a nearby lookout to bask where the surface is already warmed by the sun. Only when the body temperature reaches 36°-37° C, is the animal fully active and ready to forage.

The ctenosaur is most active in the morning, retiring underground to escape the midday heat, and often has been seen in the afternoon lying in burrow entrances or back in the tunnels awaiting more favorable lower temperatures.

Each lizard defends its home burrow against intruders, but may use other out-

lying burrows occasionally or habitually. An individual often shifts from one home burrow to another, and collectively, the burrows are the communal property of the local population.

Social Behavior: Territoriality in *Ctenosaura similis* involves exclusion of others from home burrows and basking places, and maintenance of spacing. Intrusions may cause conflict, with fighting mainly between similar-sized first-year young. A threatening approach is followed by sparring, lunging, biting, and persistent clinging to any part of the opponent that the lizard can seize, while writhing or rolling in an effort to break the other's grip. No noticeable damage was noted from such encounters.

Doubtless the most severe fighting is between large males, but is infrequent because of their relatively small numbers and wide spacing. Over a period of 11 months, Henderson (1973) observed no overt interactions between several adult males that lived beneath the same building on the outskirts of Belize City. There seemed to be mutual avoidance of confrontations by maintenance of spacing. However, when an outsider was brought in and tethered, he was promptly attacked by a dominant resident. After a series of struggles with intervening pauses for rest, the resident male gradually abandoned his attempts to oust the tethered intruder and the latter, when released, remained in the vicinity, taking possession of the burrow and basking site of the resident whom he had outlasted in the territorial confrontation.

The adult females seen always maintained spacing of at least several meters. As in other iguanids, *Crotaphytus* (Fitch, 1956), *Sceloporus* (Blair, 1960), and *Uta* (Tinkle, 1967), there is probably mutual aversion and hostility among females, but with aggressive behavior relatively weak. No female fighting nor pursuits were observed. Adult males were often seen in "consort pair" associations with females that seemed to be based on mutual attraction, but at any time the polygynous male might wander away from his consort and find another temporary mate. Formation of harems was probably prevented by mutually agonistic responses of females.

Each individual, regardless of sex or size, has a territorial center with one or more burrows or basking sites, but territorial boundaries are not well defined. The ctenosaur may spend much time basking at one or a few spots, and finally may move on to a different location without ever having used most of the apparent territorial area near its burrow and lookout. Often, food in the form of succulent vegetation is so abundant that the lizard does not need to spend much time in active foraging nor to venture far.

Where food is abundant, but choice retreats and basking sites are scarce, territories may be partly superimposed, with the same rocks or burrow used by two or more ctenosaurs at different times. Even in such congestion there is not much actual conflict. A smaller, weaker individual automatically avoids a larger, more powerful neighbor and is generally ignored by him. Evans (1951) described social behavior in a colony of *Ctenosaura pectinata* in central Mexico, living in a rock wall around a bean field. Each adult male controlled a section of the wall and adjacent areas, ordinarily excluding other adult males. However, perhaps as a result of abnormal overcrowding, there was much overlapping of territories, and a hierarchical system was superimposed on that of territoriality. A "despot" Alpha male could violate the territory of any other individual with impunity, although in such transgressions mutual threat displays were exchanged between the intruder and the resident. Likewise, other territorial males encroached on

the territories of lower ranking individuals. Many subordinate individuals were unable to maintain territories, and avoided the large dominant males.

The somewhat different social structure in the population that we observed at Belize probably resulted from the different situation, rather than specific differences between *C. pectinata* and *C. similis*. At the Belize City cemetery, the relative uniformity in size and distribution of the gravestones that provided shelter, dispersed the ctenosaurs, but at Evans' study area in Mexico, the lack of shelter, except in crevices in the rock wall, concentrated them, leading to frequent, stressful interactions.

Like most other iguanids (Carpenter, 1965), *Ctenosaura similis* displays by stereotyped, species-specific bobbing movements that substitute for actual fighting in most encounters. Henderson (1973) observed and described the display at Belize City consisting of 10-12 vertical bobs of the head with changing rate and amplitude; first, the head was slowly raised to the maximum possible height and then more rapidly lowered; 2 or 3 lower and faster bobs followed, and finally there were 2 or 3 short, quick, upward jerks. The display was often elicited by the sight of a potential rival, and might be given by females and immatures as well as adult males. Also, displays might be elicited by potential threat, such as the approach of a person. At other times the display was given in the absence of any obvious external stimulus, but seemed to reflect excitement or potential danger. It might be given just before or after a shift to a new location.

Movements: Taylor (1956), describing the habits of the species in Costa Rica, wrote: ". . . they may forage a hundred yards or more in varying directions." However, forays are usually less than 100 yards from the burrow as indicated by the homeward dashes of those disturbed in the open by a pedestrian or vehicle. A male in sexual search, a female in search of a site for egg-laying, or a lizard lured by some preferred food in the season of scarcity may venture farther than usual. More often, the same individual will be seen time after time at approximately the same spot. Henderson (1973), observing a small colony in the vicinity of a school building on the outskirts of Belize City, found that most activity is within 1-5 m of the lizard's burrow, but he noted one adult male 88 m from its burrow and recorded several other movements, up to 25 m. Fitch (1973) individually marked many juveniles, mainly in June and July, and recorded 16 recaptures in new locations after periods of weeks. Four relatively long movements were 131, 55, 49 and 46 m; the remaining 12 averaged 10.4 m (4-16).

From 2-7 March 1976, we made observations at the Belize City cemetery on a colony of 49 ctenosaurs. The cemetery was approximately 610 x 200 m bordered on each side (north and south) by a mangrove swamp, and on its west end tapered almost to a point, with a crossroad, swamp, and dense vegetation truncating the lizards' habitat, while at the east end it was bordered by buildings on the edge of Belize. Thus, the population was effectively isolated. Individual movements were further restricted by a well travelled road that bisected the cemetery lengthwise from east to west, and we saw no ctenosaurs venture onto the road. The lizards of this colony, being free from molestation by humans and conditioned to frequent passers-by, were relatively tame and could be easily approached, sometimes to within 1 m, and they could be individually recognized by a combination of size, sex, and peculiarities of color, pattern, tail regeneration, behavior and location. Each lizard had a favorite spot for basking, usually on a tombstone, and had a retreat, usually within or be-

neath the stone. Most of the tombstones were concrete slabs approximately 2 x 1 x .5 m and many were old, weathered and broken with holes or cracks providing access to the hollow interiors.

Individual ctenosaurs were recorded from 1 to 19 times, but on nearly half the occasions (N=120) were seen at the same place. Movements of less than 3 m were disregarded, because the combined retreat and basking site often spanned approximately this distance. For each ctenosaur movements were recorded as radii between the home base and outlying points visited. For 121 records average was 24.4 m (adult males, 43.0 m, N=22; adult females, 22.55 m, N=38; first-year young, 18.7 m, N=61). Each adult male usually stayed within 1 or 2 m of an adult female. Any ctenosaur, regardless of size or sex, might shift to a different lookout and usually there was a nearby escape shelter.

Use of a specific area by an individual ctenosaur does not conform well with the concept of a typical home range: "The area over which an individual animal habitually travels while engaged in his usual daily activities" (Dice 1952). The ctenosaur spends most of its time at one place and may not stray far from that center while food and other requirements are readily accessible. Feeding and other activities concentrate in the vicinity of the lookout and shelter; degree of utilization is proportional to distance from that home base. The more remote parts of the area that are within the ctenosaur's foraging radius tend to be little used, but outlying, alternative, secondary lookouts with associated shelters permit more thorough use of the area.

For each of the main groups—adult males, adult females and first-year young—radii tend to form a graduated series from the minimum to the maximum. Relatively short movements were most numerous and longer movements fewer. Several of the movements (4 of 22 for adult males, 3 of 38 for adult females, and 3 of 61 for immatures) were abruptly longer and may represent either exceptionally large home ranges or shifts in range. Excluding these few extra long movements, the maximum radii were 58.0 m for adult males, 38.2 for adult females and 48.2 m for immatures. These radii represent circular areas of 1.051, .457 and .731 hectares, respectively.

Food Habits: Although mainly vegetarian, ctenosaurs are known to have taken some animal food including grasshoppers, frogs, young of their own species, a skink, rodents, young chicks and various small birds, a bat and even human feces (Alvarez del Toro, 1960; Tamsitt and Valdivieso, 1963; Taylor, 1956; Fitch et al., 1971; Henderson, 1973).

In February, March and April 1976, we examined 146 stomachs of ctenosaurs collected in western Nicaragua (Table 1). Green foliage from both herbs and trees comprised most of the diet, being present in 76% of stomachs. Succulent plants were relatively scarce in the dry season, especially in the open and barren roadside situations where many ctenosaurs were found. Coarse, seral weeds were often eaten, as they were the most available source of plant food. Many of the lizards living along the edges of cotton fields ate leaves of cotton plants (*Gossypium*). Leaf buds and newly grown tender leaves of trees also made up much of the foliage eaten. A tree about 10 m high in a roadside strip north of Chinandega had lost its foliage when scorched by a grass fire, and new leaf buds were opening at the time of our field work in March 1976. These new leaves seemed especially attractive to ctenosaurs, as we saw several in the tree and shot two, but on the return trip later the same day we saw four, of different sizes, in the tree.

Nearly all flower material in the 146

TABLE 1

Food of Ctenosaurs; Contents of 146 Stomachs from Western Nicaragua February, March and April 1976

	Leaves	Flowers	Fruits	Seeds	Misc. Plants	Inverte-brates	Verte-brates	Feces
Total samples (146)								
Occurrences	111	86	22	11	7	29	11	1
% sample weight ..	47.1	26.2	9.4	4.0	2.3	3.0	4.1	3.9
Adults (73)								
Occurrences	54	45	9	9	5	8	5	1
% sample weight ..	45.2	23.2	10.5	5.5	3.2	2.1	3.8	6.5
Young (73)								
Occurrences	56	42	13	2	1	21	6	....
% sample weight ..	49.0	31.0	8.0	.1	.5	4.8	5.0	....

stomachs was from trees, of kinds which bloom when they are leafless at the height of the dry season. Most were legumes and were yellow, pink or white in that order of frequency. Trees with either flowers or tender foliage sometimes lured ctenosaurs beyond their usual foraging radii. Miscellaneous plant material in the stomachs included stems, and some material too much digested to be recognized in any of the main categories.

Vertebrate prey included small cricetid rodents, *Oryzomys, Scotinomys* (five stomachs), small lizards probably *Sceloporus* and/or *Cnemidophorus* (in two), a partly digested tail of a small ctenosaur (in one) and 9 small lizard eggs probably of *Sceloporus* or *Cnemidophorus,* or possibly *Ameiva* (in one). One adult ctenosaur had a ctenosaur egg, still undigested and with shell intact in its hind gut and another had eaten three such eggs. The presence of such active prey as mice and lizards, and presence of eggs that would have been deposited in burrows, indicate that some of the prey is obtained by digging.

Cannibalism of sorts is indicated by the eating of ctenosaur eggs and tail. Henderson (1973) noted that habitat separation relieves the young from predation by adults. Newly emerged hatchlings may overlap the adults' habitat more than do the scansorial juveniles a few weeks later. However, the active hatchlings are so swift and shy that most apparently escape predatory adults. Young that are several months old become less scansorial and more like adults in habits. They have doubled or even tripled in length, and are larger than the food objects that adults normally take. First-year young that lived in the areas controlled by dominant males occupied lookouts only a few meters from them, but instantly fled when the adults moved toward them.

Invertebrates found in stomachs included 2 lycosid spiders, beetles, butterflies, moths, wasps, bees, dipteran flies, hemipteran "bug," leafhoppers and a grasshopper. Some of the smaller insects made up insignificant proportions of the stomach contents, and probably were ingested secondarily on flowers or other vegetation that the ctenosaurs were eating. Invertebrates were less prominent in the food of the adults than in that of the first-year (8-10 months old) young, although these young were much like adults in habitat and behavior.

Younger, smaller ctenosaurs are much more insectivorous. Near Pisté, Yucatán,

TABLE 2

REPRODUCTIVE STATES OF ADULT FEMALE *Ctenosaura similis* IN FEBRUARY, MARCH AND APRIL, 1976

		PERCENTAGES OF FEMALES HAVING:			PERCENTAGES OF FEMALES HAVING:		
	MEAN SIZES OF OVARIAN FOLLICLES IN INDIVIDUAL FEMALES	OVARIAN FOLLICLES VS.	OVIDUCAL EGGS	*N*	OVIDUCAL EGGS OR LARGE FOLLICLES VS.	RECENTLY LAID	*N*
1-10 Feb.	1.5,4,5,7.5,8,9,10(in 3) 12(in 6),15 17,18	90	10	20	100	0	96
11-20 Feb.	.....	....	....	....	....	....	....
21 Feb.-1 Mar.	5,11,14,16,16	27	73	22	100	0	90
2-11 Mar.	15.5	14	86	7	100	0	22
12-21 Mar.	.....	....	....		93	7	160
22-31 Mar.	.....	....	....		78	22	32
1-10 April	.....	....	....		6	94	16
11-20 April	.....	....	....		....	100	13
21-30 April	.....	....	....		....	100	11

Maslin (1963) found stomachs of several juveniles (55-64 mm) filled with insects including fairly large grasshoppers. Allen Porter collected 16 young that probably averaged about 3.5 weeks old (57-80 mm) near Laguna Asososca, León Province, Nicaragua, 28 July 1976, and 15 of the stomachs had insect remains: 23 beetles (scarabaeid, chrysomelid, elaterid, coccinellid), 6 lepidopteran larvae, 3 leafhoppers, 3 ants, 1 gryllid cricket, 1 butterfly and 1 beetle grub. For 32 of the prey items sufficiently intact to be measured or estimated, average length was approximately 10 mm, and prey weight averaged a little less than .09 g. These juvenile ctenosaurs weighed a little less than 10 g on the average, hence prey weight was most often less than 1 per cent of body weight. Although 60% of the items were beetles, some of the prey was of active, swift-moving kinds. Ten of the 16 stomachs had plant material (foliage in 9, yellow flowers in 1, berries in 1) and 59.0% of the food weight was vegetation vs. 41.0% insect prey.

In gardens and cultivated fields ctenosaurs damage plants by nipping off buds, flowers, fruiting heads and tender leaves. Young bean plants are especially liked. Damage may be substantial, and as a result ctenosaurs are generally considered pests and are killed at every opportunity by agriculturalists. Doubtless at some times and places control measures are justified, but harm done to crops seems fairly trivial, weighed against the benefits accruing from utilization of the ctenosaur for food and sport.

Reproduction: Like most other iguanids, *Ctenosaura similis* is oviparous, laying a single clutch of eggs, annually. Early in the dry season in January and February fat bodies are large and ovarian follicles grow rapidly. Follicles are ovulated when they have attained a diameter of 15-18 mm. Table 2 indicates that in the first 10 days of February, 2 of 20 females examined had already ovulated, and 18 contained enlarging follicles, but in 15 of this group follicles were still not mature. In the last 9 days of February (and 1 March) 16 of 27 females had ovulated, 2 others had mature follicles, and three had follicles that were still short of mature size. The last recorded as still having follicles was ex-

amined on 10 March. In the last 10 days of March, 7 females dissected had recently oviposited and 25 still had mature oviducal eggs, but all of the 16 dissected in early April were already spent. These records indicate that in 1976 in western Nicaragua, at least, the peak of ovulation occurred in mid-February, and the peak of ovipositing was in late March. Hence, eggs were retained in the oviducts for approximately 5 weeks. Earliest and latest dates recorded for females with oviducal eggs were 4 February and 2 April, respectively. Individuals vary 3-4 weeks in the timing of their reproduction, but *Ctenosaura similis* has a much more concentrated breeding season than any other Middle American lizard that has been studied.

Number of eggs per clutch, determined from enlarged follicles and from oviducal eggs in unlaid clutches of the females dissected in February and March 1976, averaged 43.4 (12-88, N=69). The maximum of 88 distinguishes *C. similis* as one of the more prolific of all lizards, even more so than viviparous species. The wide range of variation between females in numbers of eggs is especially remarkable, and is strongly correlated with age and size of the individual.

In Table 3, reproductive females are divided into 8 size-classes which are believed to be the most plausible bases for cohorts in successive annual age-classes, taking into account the known growth rates of marked individuals and the fact that each annual cohort in a stable natural population is somewhat less numerous than the next younger group. Within each of the female size-classes in Table 3, the clutch size is much less variable than for the group as a whole, and the mean increases from approximately 22 eggs per clutch in the smallest (two-year-old primiparae) to approximately 70 in the largest adults (8-year olds).

The smallest clutch recorded (12) belonged to the smallest ovigerous female of 191 mm snout-vent (s-v) and the largest clutch (88) belonged to one of the four larger females dissected (338 mm s-v). However, a few females deviated markedly from the average clutch size for their size-group, indicating that factors other than body size may strongly influence the number of eggs.

For 40 females in which weight of unlaid oviducal eggs as well as total weight was recorded, clutch weight averaged 21.65% of the total (15.5-36.9%). For the different size-groups of females, averages approximated that of the entire group, with

TABLE 3

Adult Female Ctenosaurs That Were Measured, Grouped in Size-Classes That Correspond with Possible Age-Classes, Showing Correlation of Clutch Size with Size of Female

Size-Class mm S-V	Number measured	Estimated Age (Years)	Clutch size (means and extremes)
191-250	63	2	21.688 ± 1.164 (12-27 in 16)
251-269	51	3	36.000 ± 1.414 (29-41 in 8)
270-284	46	4	40.900 ± 3.321 (29-63 in 10)
285-299	41	5	42.428 ± 2.852 (29-51 in 7)
300-310	37	6	51.571 ± 2.927 (30-66 in 14)
311-326	25	7	61.833 ± 3.534 (49-74 in 6)
327-340	17	8	69.500 ± 3.359 (59-88 in 8)
341-347	3	9	.....

no discernible trend toward greater reproductive effort in larger females. In the ctenosaur, the "reproductive strategy" as defined by Tinkle, Wilbur and Tilley (1970) differs from strategies of most tropical lizards (but resembles that of various Temperate Zone lizards) in delayed maturity and in the production of a single annual clutch. It differs from most other lizards, but resembles some other giant iguanids, teiids, and varanids of tropical mainlands in its extremely large clutch, and in low ratio of egg- and hatchling-size to adult.

Fat deposits in the posterior ends of the abdomens were bright yellow and were especially conspicuous in females that had not yet ovulated. In 15 of these females abdominal fat bodies ranged in weight from 4 to 54 grams (.5 to 6.5 per cent of the total weight), with a tendency for those with smallest follicles to have the largest fat bodies. Evidently the fat bodies provide much of the sustenance that permits rapid enlargement of the follicles as yolk is deposited. In three females with approximately full-sized follicles (16-17 mm in diameter), fat bodies averaged 5 per cent of total weight; in nine females with follicles 12-15 mm in diameter, fat bodies averaged 48 per cent of the follicles' weight; and in two females having follicles 10-11 mm in diameter, the fat bodies averaged 169 per cent of the follicles' weight. In females that had ovulated, fat bodies were much shrunken, and in most instances weighed less than one gram. Figure 1 shows the relative weights of the fat bodies and the ovaries in females with enlarging follicles.

Growth: Typical hatchlings are between 55 and 60 mm snout-vent, but some are slightly larger or smaller. As indicated, individual females vary from three to four weeks in the time of laying, so that the earliest hatchlings are as much as 25% longer than their original length by the time the latest appear. In older young, the size difference increases as some make better growth than others. The largest in each of 18 series of 9 to 51 young (Tables 4 and 5) averaged 138.5% of the lengths of the smallest. In series that average more than a month old, the largest may be 50% or more larger than the smallest.

Early growth is best shown by ten series captured at four localities in northwestern Costa Rica in 1968 and early 1969 (Table 4). There were five successive samplings at Playas del Coco and three at Boca de Barranca. Evidently there was some difference between these localities in hatching time, from the first week of May (Boca de Barranca) to the second week (Playas del Coco) or third week (Finca Taboga, Quepos). Hatchlings were first seen on 1 May at Quepos. A single hatchling was seen on 14 May at Taboga; seemingly hatching was just beginning there. Average length gain s-v is usually approximately 4 mm per week or a little less for the first few weeks, but then slows to somewhat less than 3.5 mm per week.

Six young marked in late May and recaptured after intervals of 31 to 36 days, made an average gain of only 2.1 mm per week, probably due to temporary stunting from the adverse effects of toe-clipping. Two other young were recaptured after longer intervals, when they had fully recovered from the adverse effects of marking. From 1 July 1968 to 12 February 1969 one grew from 86 to 143 mm and from 26 August 1968 to 4 February 1969 the other grew from 95 to 170 mm. These gains indicate average growth rates of 1.76 and 3.39 mm per week, respectively, over periods of 32 weeks and 23 weeks.

The lizards of the four Costa Rican localities listed in Table 4 range from 9°25′ to 10°35′ North Latitude and have breeding schedules several weeks advanced over those occurring in more northern parts of

TABLE 4

Sizes of Juvenile Ctenosaurs on Various Dates At Costa Rican Localities, Showing Early Growth

Date	Locality	Mean Length S-V (mm.)	N	Estimated age (weeks)	Estimated average gain (mm.) per week since hatching
20-23 May	Playas del Coco	59.1 (56-63)	24	1	4
27-30 May	Boca de Barranca	70.9 (57-82)	51	3.5	4.2
20 June / 1-3 July	Quepos	76.1 (60-90)	19	5	3.4
29-30 June	Boca de Barranca	83.9 (63-109)	30	8	3.8
7 July	Finca Taboga	87.2 (73-107)	19	7	4.5
9-10 July	Playas del Coco	78.1 (63-97)	21	7	3.3
14-17 Aug.	Playas del Coco	95.5 (78-107)	9	12	3.3
20-30 Aug.	Boca de Barranca	103.9 (80-114)	19	14	3.3
23-26 Aug.	Playas del Coco	104.1 (84-127)	15	13	3.3
4-7 Feb.	Playas del Coco	147.5 (120-165)	12	35	2.6

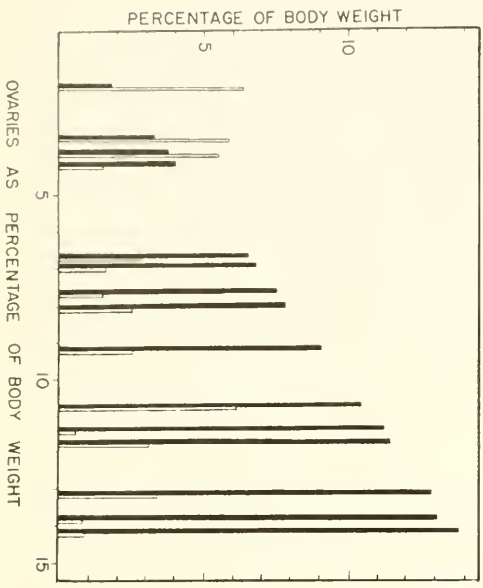
the range. Henderson (1973) found that the young first appear in mid-June in Belize. Table 5 shows average sizes of series of young collected in various parts of the range, with series arranged in order from latest to earliest calculated hatching dates. The data indicate that in some areas hatching may be delayed as much as two months beyond that characteristic of northwestern Costa Rica in lowland areas. The

TABLE 5

Sizes of First-Year *Ctenosaura similis* at Various Localities and Dates, Showing Retardation of Schedules Northward and at Higher Elevations.

Locality	Latitude & Altitude*	Mean Length S-V	Range	N	Date of collection	Estimated average hatching date
Tenorio, Guanacaste, Costa Rica	10°37′(650m)	77.25	(72-87)	4	8-23-52	18 July
Tilarán, Guanacaste, Costa Rica	10°28′(562m)	81.0	.....	1	8-15-54	11 July
Pisté, Yucatán, Mex.	20°44′	63.0	(53-71)	22	7-20&21-62	7 July
Isla de Ometepe, Lago de Nic.	11°32′	77.7	(65-92)	18	7-30-8- 1-	3 July
Lago Asososca, León, Nic.	11°26′	70.4	(57-80)	16	7-28-76	3 July
Isla de Maiz, Nic.	12°07′	57.5	(60-75)	11	6-29&30-64	19 June
14 km E Rivas, Rivas Nic.	11°26′	80.6	(88-75)	11	7-20-64	9 June
Managua, Nic.	12°08′	66.8	(60-80)	9	6-20&21-56	3 June
Managua, Nic.	12°08′	54.2	(49-59)	9	6-3&4-56	1 June
S. Antonio, Chinandega, Nic.	12°32′	73.7	(63-94)	23	7-5 to 11-64	1 June

* Near sea level, except where otherwise indicated.



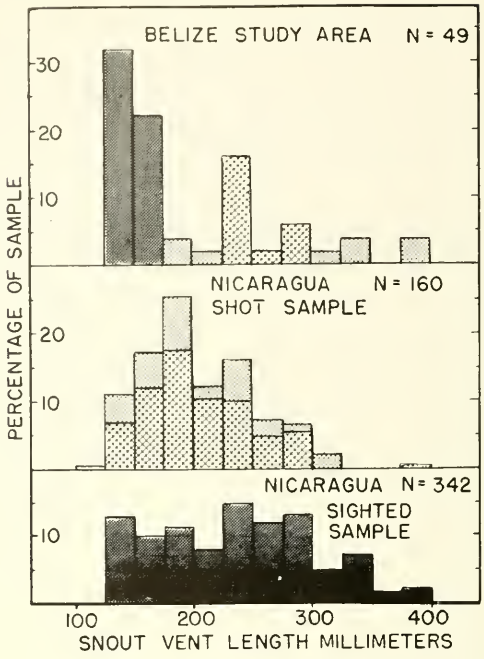


FIG. 1. Relative weights of fat bodies (open columns) and complements of ovarian follicles (solid columns) in 15 female ctenosaurs having their follicles in different stages of growth.

FIG. 2. Size-classes in three population samples of *Ctenosaura similis;* stippled columns represent males, cross-hatched columns represent females and shaded columns represent individuals of undetermined sex.

later dates were for Tenorio and Tilarán, Costa Rica, near the localities of Table 4 but in the relatively cool climates of montane areas. The next were those from Yucatán 1070 km north of the Costa Rican localities. Isla de Ometepe in Lago de Nicaragua and Isla de Maiz in the Caribbean, having relatively cool climates moderated by surrounding water, are also late. Hatching at various localities in western Nicaragua (Rivas, Isla de Ometepe, Managua, Lago de Asososca, San Antonio) is 2 to 6 weeks delayed beyond the time of hatching in the Guanacaste lowlands.

Although the annual schedule of reproduction and growth differs by only a few weeks in different parts of the range, the differences may be critical. The species thrives best in the relatively hot and seasonally dry climates of western Nicaragua and northwestern Costa Rica. In regions with more precipitation, less insolation, and lower air temperature, there is a cumulative retardation; eggs mature later, laying is delayed, incubation requires more time, and the young make less rapid and consistent growth.

Of 16 presumed second-year females, 204-250 mm s-v, collected in western Nicaragua from 6 February to 22 March 1976, 13 were reproductive, having enlarged follicles (4 females), oviducal eggs (7 females), or corpora lutea and enlarged oviducts indicative of recent egg-laying (2 females). The remaining 3, having lengths of 220, 215 and 209 mm s-v, had minute ova and small oviducts. Thus, 18.7% of females in the two-year old size-class were non-reproductive. In other parts of the range where climate is less favorable, postponement of sexual maturity until the third year may be the mode, with consequent major loss of reproductive potential.

In western Nicaragua, 6 February to 5

April 1976, first-year young of 170-189 mm length (females) and 190-197 mm (males) were more numerous than larger or smaller young and probably were modal for their age-group of about 8-10 months. Average growth rates (s-v) from the time of hatching are calculated at about 3.1 mm per week for females and about 3.5 mm for males. However, some young, presumably of approximately the same age, were still as small as 127 mm (female) and 135 mm (male), indicating a wide range among individuals. First-year and second-year young apparently overlap in size mainly in the range 190-200 mm for females and 235-250 mm for males. If 200 mm is considered the upper limit for first-year females (in our sample of 160), 53 fall in this age-class, with a mean length of 171 mm. For males, a criterion of maturity that may separate second-year adolescents from first-year young is length of spines of the dorsal crest. These spines are long and prominent in adult males, but low and flattened in females and juveniles. Individual males of 238, 241 and 248 mm and all that were smaller had short spines (2.5 mm or less), whereas individuals of 239, 240 and 247 mm, and all but one that were larger, had relatively long spines (5 mm or more). If males up to, but not including, 240 mm are considered first-year young, the sample includes 39 of them which average 188 mm.

At the end of the first year, males average aproximately 10 per cent larger than females, and as adolescents and adults they grow about twice as fast as females, judging from maximum lengths s-v of 489 (male) and 347 (female). As in most reptiles, growth continues throughout life with allometric changes in proportions. Head shape, especially, is subject to progressive change in males. With advanced age their jaws become elongated and heads are widened posteriorly (Fitch and Henderson, 1977).

Population Density: In the cemetery at Belize City, covering approximately 9.66 hectares, we recorded 49 ctenosaurs with total biomass calculated at 16.13 kg (1.67 kg per ha), adult females making up 45.2%, adult males 40.8% and first-year young 14.0%.

Although the cemetery superficially seemed to provide a fairly uniform habitat, the lizards were distributed with obvious clumping. As there was a surplus of food, the most obvious factor controlling distribution was relative age of gravestones in different parts of the cemetery. Where a high proportion of the stones were old, weathered, cracked, or partially collapsed, there were more hiding places for the ctenosaurs than there were where the stones were relatively new. Groups of graves that were enclosed by iron fences also seemed to provide security that made them especially attractive. There were four solitary individuals (subadult male, first-year young and two adult females) and 11 associations of from two to 10 individuals. The largest associations, with 10, eight and seven individuals, each had adults of both sexes and young. In associations of four, all were young. Associations of three had all young in one instance and had a pair of adults and a juvenile in another. Associations with only two lizards consisted of female and young in two instances, both young in two instances, subadult male and young in another.

Spacing between neighboring groups, or between groups and solitary individuals, averaged 74.5 m; within groups spacing of individuals averaged 25 m. Except in the case of consort pairs, it is doubtful whether individuals were attracted to others and the clumping observed may have been a result of the unevenly distributed resources, especially suitable shelter.

Taylor (1956) wrote that a colony of 10 or more ctenosaurs might be based at one large tree with hollow trunk or limbs. We found such a concentration would be un-

usual and would consist largely of immatures. An adult male and female often remain in close proximity for periods of days; otherwise individuals tend to be well spaced.

In Nicaragua, where ctenosaurs are extensively hunted, population densities comparable to that in the Belize City cemetery are unusual, but even higher concentrations were observed along roadsides, field edges and gullies in Chinandega Province north of Chinandega and along the Honduran border northeast of Palo Grande. In Costa Rica, similarly dense populations were observed at Finca Taboga in Guanacaste Province.

Because egg clutches are large, juveniles sometimes occur locally in high population densities. They tend to maintain spacing; aggressive displays and fights hasten their dispersal after hatching.

Population Structure: Ctenosaura similis normally requires nearly two years to attain sexual maturity, and individuals may survive and continue to grow for many years subsequently. A natural population therefore consists of many discrete annual age-classes, each larger in size and less numerous than the next younger group. Broods are large, but early mortality is heavy. Ratios of juveniles to older individuals are distorted by behavioral differences. Young that are several months old have become much like adults in behavior and habitat, and their cohorts have already sustained their heaviest losses.

Three separate population samples were obtained by different methods in the period February to April 1976, when first-year young were mostly in the age-range 8-10 months and had grown in linear dimensions to approximately three times their original size, and to approximately half the size of adults. These three samples (Fig. 2) show important similarities and differences, the latter probably reflecting biases inherent in the sampling techniques.

A sample of 160 ctenosaurs was obtained by hunting with a .22 rifle from a vehicle on roads and highways of Chinandega, León, Managua, and Chontales Provinces in Nicaragua. We attempted to obtain a random sample. However, there is a possibility of bias resulting from greater wariness of old individuals and/or from more persistent late afternoon activity in yearlings and gravid females. Numbers and percentages of different classes in the sample were as follows: first-year young 86 (53.6%); probable second-year adolescents 49 (30.6%); large adult males 7 (4.4%); large adult females 18 (11.3%). There were 32 males (135-220 mm) and 54 females (127-200 mm) in the group of first year-young, and 14 males (221-298 mm) and 35 females (201-250 mm) in the supposed second-year group. The adult males ranged from 299-400 mm, adult females from 253-295 mm. It is noteworthy that females constituted two-thirds of the total sample, and were from 63 to 72 per cent in different age-classes. Behavioral differences between adult males and females might cause some bias, but in first-year young sexual differences in behavior are small, if they exist at all, and would not result in significant bias. We therefore conclude that the sex ratio is strongly skewed in favor of females from the time of hatching.

A larger sample of 342 ctenosaurs was tallied from a vehicle during drives in the same parts of Nicaragua involved in the preceding sample. These animals were not handled; snout-vent lengths were merely estimated, and usually sex was not determined. Sometimes estimates were made simultaneously by two or three persons and a compromise figure was agreed upon. Often the same animal was first estimated and then shot and measured, providing opportunities for adjustment and refinement of the estimates. However, accuracy

varied and for those only glimpsed briefly the range of error must have been relatively large. Large adults were better represented in this "sighted" sample, and first-year young were only 37.5% (vs. 53.6 in the "shot" sample).

A third population sample consisted of the 49 ctenosaurs observed at the Belize City cemetery 2-7 March 1976. Although only one was captured and measured, size estimates were made by observing them at close range and were checked repeatedly for most of them. Sex was readily distinguished in the full-grown lizards and tentatively distinguished in second-year adolescents (by head shape proportions, and elongated spine-like scales of the dorsal crest in the males) but could not be distinguished in first-year young. The latter averaged markedly smaller than first-year young in western Nicaragua at the same time of year, and unlike those young they did not overlap the second-year size-class. Of the 49 total, 27 (55.0%) were first-year young. Of the remaining 22, 8 (36.3%) were males and 14 (63.5%) were females. Five of the 8 males were large (320-400 mm) dominant individuals.

Figure 2 compares distribution of size-classes (with 25 mm interval) in each of the three samples. It shows that there is a continuum in size from the smallest first-year young to the largest adult males. Main concentrations are those of the first year young (150-200 mm in Nicaragua, but smaller in Belize) and of young adults (mostly females) 226-250 mm.

EXPLOITATION

The ctenosaur has delicate, tasty, white meat and in México and Central America it is much sought as an article of food. It is normally preferred over the iguana (*Iguana iguana*) where both occur together. However, in Belize only iguanas are eaten. In that region ctenosaurs are highly localized and because they are much in evidence in the Belize City cemetery, are regarded with a superstitious aversion. Called "wish-willys" by the English-speaking black Creoles, these reptiles are believed to feed upon corpses in the graves.

Elsewhere the species has probably been used for food since pre-Columbian times, but degree of exploitation varies locally. In parts of western Costa Rica where the ctenosaur is abundant, it is subject to little hunting, but in Nicaragua, El Salvador and Honduras it is intensively exploited and local populations have rapidly dwindled. We questioned many *campesinos* in western Nicaragua to obtain information concerning the time and amount of reduction. There was almost universal agreement that drastic reduction had occurred because of overhunting, but there was much difference of opinion, even in the same general area about the time of reduction. Many of the older *campesinos* who were questioned said that ctenosaurs formerly were numerous, but had become so scarce that now they are seldom hunted or eaten. Among 21 informants who had definite impressions as to when reductions had occurred, figures varied from 1 to 30 years, but 3 years was the most frequent estimate (6 instances) and the average was approximately 8 years.

Of 87 people questioned, 70 (80%) said they ate ctenosaurs regularly or occasionally. Most of these individuals or members of their families obtained the animals by hunting; a few bought their ctenosaurs from the hunter. Forty-nine persons made statements about the number of ctenosaurs eaten per week, which averaged 4.75. However, 17 other persons said they did not eat the meat, and 16 others who said they did (or had in the past) were vague about the amount because their use was occasional, rare or highly seasonal. Although our sample of interviews is small, and is doubtless biased in various ways it does indicate some general trends and suggests harvest

on an enormous scale. Over extensive areas of western Nicaragua the majority of *campesino* families serve ctenosaur meat once to several times weekly, and this flesh is an important protein supplement to diets that otherwise tend to be high in starch and meager in quantity.

Hunting ctenosaurs is considered sport and the species qualifies as a game animal. *Campesinos* were questioned about their methods of capture. In order of frequency mentioned, the usual methods were: with a trained dog (52), with a noose placed at the burrow entrance or manipulated on the end of a long stick (24), with a slingshot (24), with a small bore rifle or pistol (9), and with a digging stick or shovel (6). Most informants mentioned 2 or more of these methods. For those that mentioned only one method, the order and number were: dog (12), slingshot (3), digging (2), gun (2). Sunday hunting is customary, especially for persons who work during the week, as field hands on *fincas;* it is often the main outdoor recreation.

In some areas, *campesinos* from early childhood develop a familiarity with ctenosaurs and the techniques of taking them. Certain families and even communities specialize in hunting the lizards, make it their main occupation and supply the market places. The villages of Palo Grande, Somotillo and Villa Nueva near the Honduran border have many hunters who are the main suppliers of the market in Chinandega and contribute to the stocks in León, Managua, Masaya and Granada. Several other villages in northwestern Nicaragua are also important suppliers: Somoto (for Chinandega), and Rota and El Sauce (for León). Most of the ctenosaurs sold in the Mercado Oriental of Managua were said to have come from the village of San Francisco de Carnicera on the northeastern shore of Lake Managua. However, the ctenosaurs shipped from San Francisco are assembled by a dealer there from the neighborhood of Cuatros Palos and other outlying villages farther north and east, and represent the combined efforts of approximately 20 hunters. Professional hunters are especially skilled, not only in finding and capturing the animals, but in taking them alive and intact. One hunter demonstrated his technique, with a long bamboo pole having a cord noose at the end, and a bait of calf liver suspended in front of it. He told us that with his partner he left home for as much as 3 days at a time on extended hunts to areas several kilometers away, where the lizards were still relatively numerous, and both men returned heavily loaded with sacks of live ctenosaurs.

A few dozen skilled hunters are the main suppliers of the market in the larger Nicaraguan cities. They hunt on foot and their activities are concentrated in relatively small areas where ctenosaurs are abundant. Each hunter captures dozens of the animals weekly, but some men limit their hunting to the lizards' reproductive period, December through April, and seek other means of livelihood for the remainder of the year.

In February and March 1976, there were usually 1 to 5 vendors selling ctenosaurs at each major *mercado* in Nacaragua. Occasionally a vendor had between 100 and 200 ctenosaurs at one time, but usually the stock was much less— sometimes only one. The vendor normally replenished his stock with a new shipment once or twice a week. Often the shipment consisted of a mixed lot of ctenosaurs and iguanas. Some of the animals were kept in gunny sacks, while others were displayed in large wicker baskets, or were strewn over the sidewalk, immobolized by having their feet bound behind them. The live animals attracted considerable attention from passing crowds. When a new lot was displayed, prospective buyers gathered to examine and handle the animals, with brisk trading favoring egg-bearing females and large,

fleshy males. At the two *mercados* in León, live ctenosaurs were usually absent or were displayed in small numbers, but the dressed carcasses were sold at several indoor stalls. Piles of several dozen carcasses were on display on most occasions. We were told that the butchering was done at the home of the vendor, in pre-dawn hours before the *mercado* opened. At other *mercados* dressed ctenosaurs were seen in small numbers, but most of the animals were sold alive.

From the numbers of ctenosaurs appearing at Nicaraguan *mercados,* and from the statements of vendors, the aggregate weekly consumption must total hundreds of animals. Chinandega, León, Masaya, Managua, and Granada rank in about that order in numbers consumed. Many other small towns and villages participate in the ctenosaur trade, but on a relatively small scale. Some of the villages in northwestern Nicaragua that supply major *mercados* export part of their stock to El Salvador. Trucks with shipments of hundreds cross the border into Honduras from Somotillo and El Espino, Nicaragua, and hundreds more are sent by ferry from Potosí directly to El Salvador at Puerta Amapala. Nevertheless, the commercial harvest seems to be much less than the aggregate harvest by individuals hunting for family subsistence.

Live ctenosaurs were sold for food in 1976 at prices ranging from 1.5 Cordobas to 15 Cordobas (1 C = $0.14 US). The lowest prices prevailed in the villages of northwestern Nicaragua. There the hunters usually received 2 or 2.50 C apiece for ctenosaurs and sold them in dozen lots. In other parts of the country where the animals were less common, the hunters usually received 3 or 4 C apiece for them. The buyer usually paid 5 C at the Chinandega *mercado,* 8 (7-10) at Managua and 8-12 at Masaya and Granada. At the latter two cities, there was often an adjustment of price according to the animal's size, whereas at Chinandega the price tended to be uniform even though one animal might be as much as 5 times the bulk of another.

DISCUSSION

Ctenosaura similis is unique among American lizards in several aspects of its ecology: It has become adapted as an adult to feed upon the dominant vegetation, with the result that food supply is not generally limiting. It produces remarkably large egg clutches (mean 43.4, maximum at least 88). It is single-brooded with eggs laid late in the dry season and young appearing early in the rainy season. Its hatchlings are remarkbaly small compared with adults (about 16 per cent of female length and one per cent of female weight). Its females are much smaller than males (80% of male length and 55.6% of male weight) and are more numerous both in samples of adults and in first-year young in a ratio of about 2 to 1. Sexual maturity is attained late in the second year, and the two-year-old primiparae made up 23.2% of the breeding females and produced 10.6% of the eggs in a sample.

Although the ctenosaur is "*K*-selected" (see Pianka, 1970) in having a long life expectancy, postponing maturity till the second year, and producing a single annual brood, it is "*r*-selected" in its remarkably large clutch, in relatively small size of its eggs and hatchlings, and in its adaptation to disturbed and seral habitats. All these "*r*-selected" traits reduce its vulnerability to exploitation by humans and confer potential as a successful game animal. Over extensive areas of xeric habitat where the original fauna has been depleted by man-made changes, involving virtual elimination of the birds and mammals that were favorite game animals, the ctenosaur continues to thrive. Heavy grazing, or clearing of the land for cultivation, favor its survival and increase if there are certain essen-

tial habitat features that assure adequate shelter and a year-round food supply.

Despite its high reproductive potential and capacity to withstand hunting pressure, the ctenosaur has had its populations reduced at an accelerating rate in recent years. Mushrooming human populations have resulted in ever-increasing hunting pressure, with hunting intensified in the season of reproduction and concentrated on the gravid females, the least expendable part of the population. The reduction that has already occurred must have involved annual loss of hundreds of tons of high grade protein food in Nicaragua alone, with the prospect of increasing losses until the yield becomes negligible. Management practices that will reverse the trend are acutely needed.

It would be easy to suggest measures that would preserve remaining populations and permit their increase, but it is much more difficult to make practical recommendations. Exploitation of the ctenosaur is deeply rooted in tradition, whereas the concept of conservation is foreign to the exploiters. In the face of want, *campesinos* will not readily relinquish their presumed right to hunt ctenosaurs for food or to harvest the gravid females that should be left to replenish the population. Elimination of this potentially valuable species is deplorable and unnecessary. There are slight grounds for optimism in the fact that rural people almost universally recognize that ctenosaurs are rapidly becoming scarcer and that this decline results from overhunting.

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THE UNIVERSITY OF KANSAS
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THE CLASSIFICATION OF HALICTINE BEES: TRIBES AND OLD WORLD NONPARASITIC GENERA WITH STRONG VENATION

By
Charles D. Michener

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The Classification of Halictine Bees: Tribes and Old World Nonparasitic Genera with Strong Venation[1]

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ABSTRACT

This study segregates and describes the tribes of the subfamily Halictinae. The Nomioidini is the most distinctive, but has not usually been recognized as a tribe. The Old World non-parasitic Halictini with strong wing venation are revised to the subgeneric level. The recognized species are listed for revised faunas; otherwise trivial names are listed without indications of synonymies. American representatives of the Old World groups are included. The name *Patellapis* is resurrected for a large African group, divided into three subgenera, *Lomatalictus* n. subg., *Chaetalictus* n. subg., and *Patellapis s. str.* A related, large, African genus, *Zonalictus* n. g., is recognized. The primarily Oriental group *Pachyhalictus* is raised to the generic level and *Dictyohalictus* n. subg. is described for its African representative. *Thrincohalictus* is raised to the generic level. Only three subgenera of *Thrinchostoma* are recognized, *Eothrincostoma, Thrinchostoma s. str.,* and *Diagonozus.* For *Halictus* the usual three subgenera *Seladonia, Vestitohalictus* and *Halictus* are recognized.

INTRODUCTION

This work on the classification of sweat bees (Hymenoptera, Apoidea, Halictidae) was begun in order to provide a firmer basis for understanding halictine social evolution. The present paper is a segment in a larger study. When all the halictine groups have been included, a comprehensive account of the probable lines of descent and of the origins of sociality will be prepared.

The parasitic halictine groups were treated earlier (Michener, 1978), so that the numerous special features of parasitic genera may be excluded from further consideration. The result is important shortening of the descriptive material for the nonparasitic genera.

The three halictine tribes are characterized below. The genera of one of them, the Augochlorini, were revised by Eickwort (1969). The Nomioidini contains only a single genus and is treated below. The Halictini contains several nonparasitic genera. Two of them, possibly to be subdivided later, have the third and often the second transverse cubital veins and the second recurrent vein of the fore wing, at least in females, weakened relative to nearby veins. These genera, *Homalictus* and *Lasioglossum* (including *Evylaeus*), are excluded from the present paper and will be treated later. Also excluded from this paper are a number of strictly American genera with strong distal wing venation. These are *Agapostemon, Caenohalictus, Habralictus, Paragapostemon, Pseudagapostemon, Rhinetula,* and *Ruizantheda.* These genera are not closely related to those treated below and will be the topic of a later study by R. B. Roberts. The remaining Halictini, those with strong wing venation found in the Old World, are the principal topic of the present paper. One such genus, *Halictus,* occurs also in the New World and its variations and species in New World are included.

In the descriptive material, noteworthy characters and especially those unique to a group are italicized to facilitate rapid use. In the generic descriptions for the Halictini, the various areas or characters are numbered, to facilitate quick comparison of particular features among genera.

The lists of species given for the various genera and subgenera are not exhaustive. They contain names of species of which I have seen authentic material, plus names added from the literature when descriptive information is adequate. Many species described in *Halictus* s. l., often with no indication of group characters and sometimes compared to unrelated species that are now

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in different genera, can be placed only by re-examination of type material.

For areas such as Africa for which no revisional studies exist, all names which I have been able to place as to genus or subgenus are included in the lists. For areas included in revisional studies or catalogues, synonymous names are excluded, often even when the published synonymy postdates the revisional studies. Such catalogues or revisions are those of Sandhouse (1941) and Michener (1951) for North America, Wille and Michener (1971) for the Neotropical region, and Blüthgen (1920, 1921, 1923a, b, 1924) and Ebmer (1969, 1976b) for the Palearctic region. Revisional treatments of *Pachyhalictus* and *Thrinchostoma* are indicated in the accounts of those genera.

Specific names marked by asterisks are placed on the basis of the literature only.

Key to the Tribes of Halictinae

1. Anterior tentorial pits in clypeus, separate from epistomal suture although connected to suture by sulci; fimbria of metasomal tergum V of female not divided by longitudinal specialized area ..... Nomioidini
.... Anterior tentorial pit in epistomal suture; fimbria of tergum V of female in nonparasitic forms divided by longitudinal median area of specialized fine, dense pubescence and punctation 2
2. Longitudinal median specialized area of tergum V of female not divided by a cleft; metasomal tergum VII of male with a transverse ridge, usually carinate, forming a false apex beneath which the tergum is strongly reflexed to the morphological apical margin, surface above the transverse ridge usually with a recognizable hairless pygidial plate ..... Halictini
.... Longitudinal median specialized area of tergum V of female divided by a deep cleft in the tergal margin; tergum VII of male without pygidial plate and without transverse premarginal ridge or carina forming a false apex ..... Augochlorini

Tribe Nomioidini

This tribe consists of minute species with dull, metallic, greenish, bluish or brassy, or rarely black, head and thorax and yellow markings in both sexes, usually involving the clypeus, pronotal margin, often the scutellum and metanotum, parts of the antenna and legs, and bands across the metasomal terga.

Outer veins of forewings strong. Inner orbit rather strongly, angularly emarginate above middle. *Anterior tentorial pit at apex of sharp angle or sulcus deep into general clypeal area,* near upturned end of the large preapical transverse clypeal groove.

Male: Metasomal tergum VII without recognizable pygidial plate, but margin produced posteriorly; truncate or notched. Posterior margin thin, not reflexed anteroventrally as in Halictini. Sternum VIII with well developed spiculum as well as long apical process. Apex of sternum VI somewhat produced, but entire. Genitalia rather elongate, gonostylus longer than the rest of genital capsule, over twice as long as gonocoxite, without ventral reflexed flap, much exceeding penis valves; plane of dorsal bridge of penis valves vertical. Second tarsomere of hind leg narrowed toward base, freely articulated with basitarsus, as third is articulated to second.

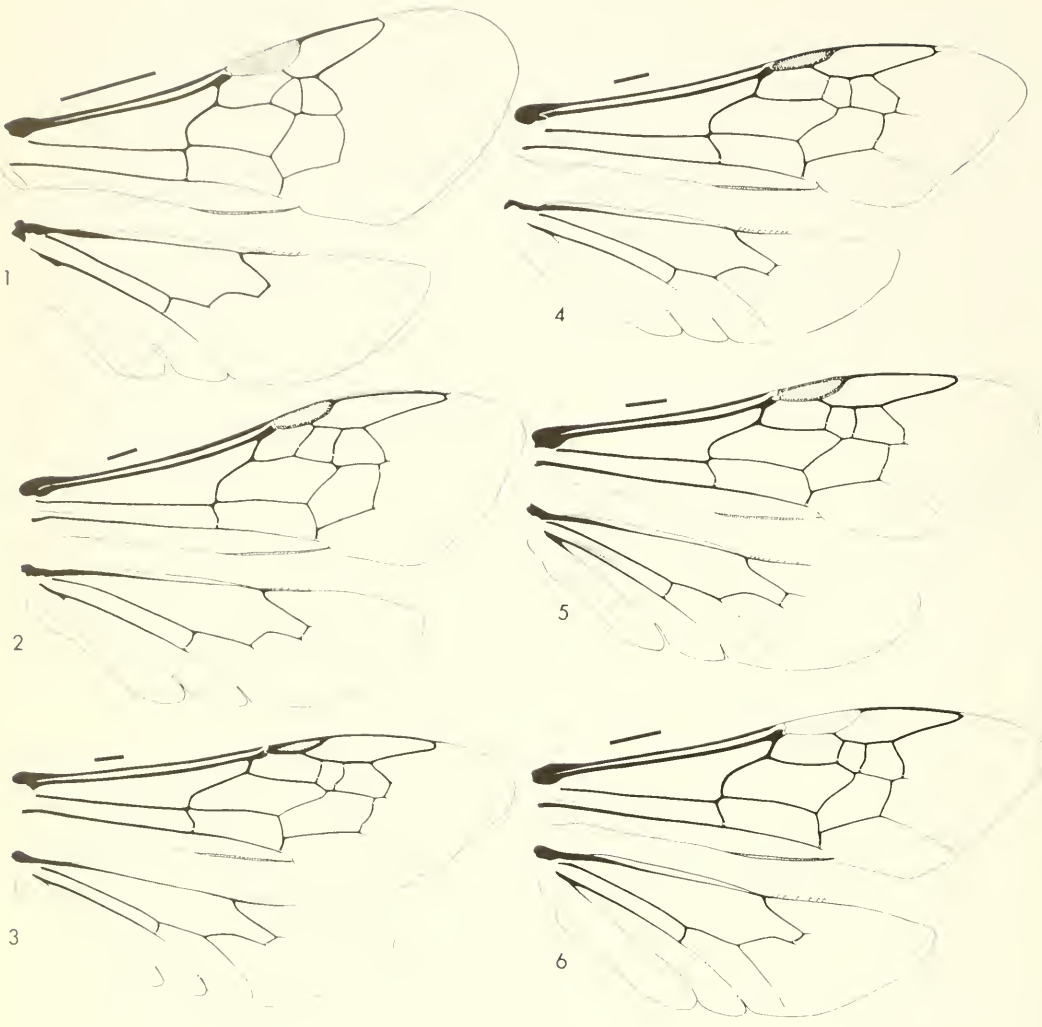
Female: Labrum not thickened, apical process minute, with few hairs, not keeled. Metasomal tergum V with apical margin and fimbria entire, without median slit or area of specialized texture or vestiture.

Genus *Nomioides* Schenck

Figures 1, 7-9

This is the only genus of the Nomioidini. It consists of minute, usually yellow and greenish black bees. A few characters that vary among genera in other tribes and that are therefore of interest in the present context are as follows:

Lower ends of paraocular areas angularly projecting into clypeus. Inner hind tibial spur of female coarsely pectinate with a very few large teeth. Strigilis ending bluntly, with radiating series of apical spines. Costal margin of marginal cell about as long as stigma, shorter than distance from apex of cell to wing tip; apex of marginal cell subtruncate or rounded. Lateral margins of metasoma with sharp angle separating dorsal from ventral parts of terga, the latter and the sterna often with long scopal hairs (angle less sharp in *N. minutissima* than in most species).



FIGS. 1-6. Wings of Nomioidini and Halictini. The scale lines represent 0.5 mm. 1. *Nomioides minutissima* (Rossi). 2. *Thrinchostoma* (*Thrinchostoma*) near *sjostedti*. 3. *Halictus* (*Halictus*) *quadrimaculatus*. 4. *H.* (*H.*) *ligatus*. 5. *H.* (*H.*) *maculatus*. 6. *H.* (*Seladonia*) *hesperus*.

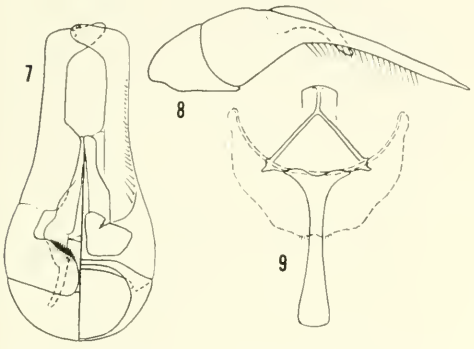
Nomioides ranges from southern Europe to southernmost South Africa, west as far as the Canary Islands, eastward to Madagascar and across Asia (north to the Caspean) to Taiwan and the Philippines, and southeast to Indonesia and Australia. It is common and represented by many species in arid and semiarid areas, but scarce and local in humid forested regions; it has not been found in New Guinea or islands to the eastward, although present in various Sunda Islands. The genus was revised by Blüthgen (1925) with a supplement in 1934.

Nomioides appears to be divisible into two subgenera, as follows:

Subgenus *Nomioides* Schenck, s. str.

Nomioides Schenck, 1866, Berliner Ent. Zeitschr. 10:333. Type species: *Andrena pulchella* Jurine, 1807=*Apis minutissima* Rossi, 1790 (monobasic).

This subgenus contains those species in which the pale, dorsal, integumental bands are on the posterior margins of the metasomal terga.



Figs. 7-9. *Nomioides minutissima* (Rossi), male. 7, 8. Dorsal, ventral and lateral views of genitalia. 9. Seventh and eighth sterna, the former shown in broken lines.

Subgenus *Ceylalictus* Strand

Ceylalictus Strand, 1913, Arch. Naturgesch., 79(A): 137. Type species: *Halictus horni* Strand, 1913 (monobasic).

Cellaria Friese, 1913 (not Ellis and Solander, 1786), Deutsche Ent. Zeitschr., p. 575. Type species: *Nomioides arnoldi* Friese, 1913 (monobasic).

Cellariella Strand, 1926, Arch. Naturgesch. 92(A):53 (new name for *Cellaria* Friese). Type species: *Nomioides arnoldi* Friese, 1913 (autobasic).

Eunomioides Blüthgen, 1937, Commentationes Biol., Soc. Sci. Fennica, 6:3 (no description or bibliographical reference). Type species: *Andrena variegata* Olivier, 1789, by original designation.

In this subgenus the pale, metasomal bands are on the median or basal parts of the terga. *Ceylalictus* is not the name generally applied to this group, because Blüthgen proposed *Eunomioides* for it. However, *Ceylalictus* has priority; moreover, *Eunomioides* was never described, nor was a bibliographic reference given. It was therefore not validly proposed. *Cellariella* easily falls into *Ceylalictus* as here understood, differing by a single venational character.

Tribe Augochlorini

This tribe is restricted to the Western Hemisphere and most of its species are strongly metallic green, blue, brassy, etc. A few, however, are weakly metallic (as is *Seladonia*) and a few almost completely lack metallic tints. Yellow or white markings are usually absent; if present they are limited to appendages, labrum, and lower half of clypeus of males.

Outer veins of forewings not weak. Inner orbit usually distinctly emarginate above middle of eye.

Male: Metasomal tergum VII without pygidial plate, without transverse premarginal carina and without zone below it reflexed to meet apex of sternum VI. Sternum VIII with spiculum. Sternum VI usually with median apical notch. Genitalia rather broad, gonostylus usually shorter than gonocoxite, without basal ventral flap; plane of dorsal bridge of penis valves horizontal so that bridge is entirely visible in dorsal view. Second tarsomere narrowly articulated to first, as third is to second.

Female: Labrum thick, except in parasitic forms with apical process bearing a strong longitudinal keel. Metasomal tergum V with median longitudinal minutely pilose or roughened area deeply notching into the prepygidial fimbria of long hairs, *tergal margin in middle of this area deeply cleft; or* in parasitic forms (*Temnosoma*), tergum V unmodified with continuous apical hairy area.

The genera of this tribe have been treated in detail by Eickwort (1969) and are not further dealt with in this paper.

Tribe Halictini

This large tribe contains most Old World Halictinae as well as many of those of the New World. Species vary from minute to large, black to brilliantly metallic green or blue, usually without yellow markings in the female (the superficially *Nomioides*-like genus *Habralictus* is an exception) and with yellow if any restricted to the clypeus, antennae, and legs in males, less commonly (*Agapostemon* and related Neotropical genera) forming metasomal bands or present on pronotal lobes.

Outer veins of fore wings often weakened. Inner orbit usually not strongly emarginate.

Male: Metasomal tergum VII usually with recognizable although often poorly defined pygidial plate margined posteriorly by a transverse ridge or carina which forms the extremity or superficial apex of the tergum, above and behind the morphological posterior margin; area (sometimes only narrow marginal zone) beyond apex of plate reflexed, normally meeting posterior margin of sternum VI, occasionally pygidial plate reduced or absent, but even in such cases posterior part of tergum VII reflexed as indicated above. Sternum VIII without spiculum. Apex of sternum VI entire. Genitalia rather broad, gonostylus usually shorter than gonocoxite, often with basal ventral flap; plane of dorsal bridge of penis valves vertical. Second tarsomere of hind leg sometimes fused to first, sometimes articulated but with articulation broader than that of third to second, sometimes narrow at base like third.

Female: Labrum thick, except in parasitic forms with apical process bearing a strong longitudinal keel. Metasomal tergum V with median, longitudinal, minutely pilose area (absent in parasitic genera) deeply notching into the prepygidial fimbria of long hairs, but *tergal margin not cleft.*

Except for *Halictus,* the genera considered here all belong to a group of genera in which the metasomal sternum IV of the male is armed with coarse and sometimes gigantic setae or bristles and frequently shortened, mostly or wholly hidden by III. Only *Thrinchostoma orchidarum* and the subgenus *Lomatalictus* of *Patellapis* (perhaps only the one species of that subgenus whose male is known) are exceptions to this feature. This group of genera is primarily African although it also ranges across tropical Asia. The presence of a membranous retrorse basal lobe of the male gonostylus in all members of this group suggests a relationship to the *Lasioglossum-Homalictus* group, *i.e.,* to the genera of Halictini with weakened distal wing venation. Such a lobe is absent in *Halictus,* although present in the Neotropical *Agapostemon* group.

KEY TO OLD WORLD NON-PARASITIC GENERA WITH STRONG APICAL WING VENATION

1. Female with margin of clypeal truncation, distal to preapical fimbria, extended downward at each side of labrum as a small, rather sharp, impunctate projection (except in some minute Asiatic species of the subgenus *Vestitohalictus* which lack such projections). Fourth sternum of male unmodified or at least without coarse, apical setae. Ventral basal process of male gonostylus absent or if present directed apically and resembling a second stylus ..... *Halictus*

.... Female with margin of clypeal truncation, distal to preapical fimbria, extending but little downward at each side of labrum, forming only a low rounded projection (except in some species of *Thrinchostoma* in which there is a strong projection). Fourth sternum of male usually shortened, commonly hidden by third sternum, nearly always with apical or subapical coarse setae. Ventral, basal process of male gonostylus present, directed ventrally or basally, forming a retrorse lobe 2

2. Apical marginal areas of terga with simple, laterally directed hairs that usually form bands that are conspicuous only in certain lights. Profile of scutum in front gently convex, rising but little above level of pronotum. Pronotum with carina separating dorsal from declivous anterior surface. Recurrent veins both entering third submarginal cell or first recurrent entering extreme apex of second cell ..... *Thrinchostoma*

.... Apical marginal areas of terga variable, but without simple, laterally directed hairs. Profile of anterior part of scutum strongly convex, so that there is a subvertical surface rising well above level of pronotum and then curving strongly or angularly onto dorsum of scutum. Pronotum medially without carina separating dorsal from anterior surface. Recurrent veins entering second and third submarginal cells, each well before apex of its cell 3

3. Malar area about as long (female) to twice as long (male) as diameter of

flagellum. Pygidial plate of male not defined. Gonostyli of male not bifurcate ..... *Thrincohalictus*

.... Malar area usually linear, rarely about half as long as diameter of flagellum. Pygidial plate of male defined at least posteriorly and posterolaterally by a carina. Gonostyli of male bifurcate, one branch sometimes slender and inconspicuous 4

4. Metasomal terga with basal bands of tomentum. Pygidial plate of male rather small. Rami of male gonostylus subequal in thickness. Hind tibia of female with outer surface largely covered with rather short, nearly erect hairs of uniform length .... *Pachyhalictus*

.... Metasomal terga without basal bands of pale tomentum. Pygidial plate of male large. Outer ramus of male gonostylus much more slender than inner. Hind tibia of female with hairs on outer surface longer, slanting, as in most halictids 5

5. First and frequently other metasomal terga usually with colored (blue, green, yellow, white) apical integumental bands. Thoracic pubescence long, plumose, usually yellowish; body almost without areas of short, whitish pubescence or tomentum as in many halictine groups. Clypeus of male often with yellow ..... *Zonalictus*

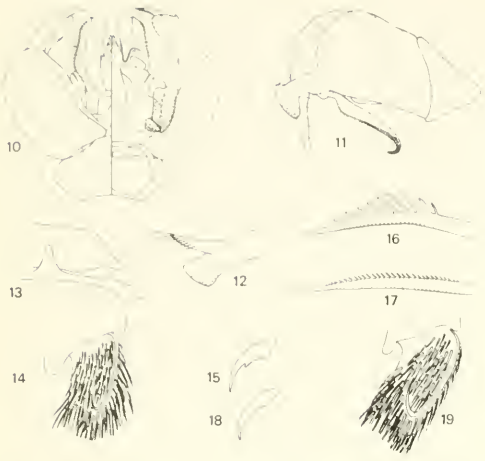
.... Tergal margins not colored. Thoracic pubescence usually shorter, less fully plumose, grayish or whitish; body often with areas of whitish pubescence or tomentum. Clypeus of male without yellow areas ..... *Patellapis*

Genus *Patellapis* Friese

Figures 10-44

The hitherto little used name *Patellapis* is here applied in a much broader sense than previously. It becomes a substantial genus of African Halictini, encompassing species that exhibit much morphological diversity.

1. Nonmetallic black (sometimes with red metasoma), small to rather large, 5-14 mm long. 2 Punctation ordinary, ground between punctures shining to dull. 3. Clypeus neither produced downward nor protuberant forward (except produced and protuberant when head is elongate, as in *P. braunsella*), less than three times (sometimes only twice) as broad as long, angle at end of truncation not or feebly produced, surface shining between punctures, uniformly gently convex. 4. Line between lower ends of eyes crossing clypeus below or above middle. 5. Malar space linear or about half as long as width of flagellum in *P. pastina*. 6. Paraocular area not extending down as lobe into clypeus, or forming an obtuse angle, or in *P. braunsella* a strong lobe. Mouthparts short (as in *Pachyhalictus*) to quite elongate; glossa in *P. braunsella* as long as face, more than twice as long as labial palpi, and postpalpal part of galea over twice as long as broad. 8. Pronotum with subhorizontal, dorsal surface medially about one third as long as flagellar width, often densely tomentose, margined anteriorly by declivity of pronotal surface, not by carina or sharp angle. 9. Dorsolateral angle of pronotum obtuse, not lamellate or strongly carinate, a weak carina often extending across posterior lobe of pronotum, a rounded ridge extending downward from dorsolateral angle. 10. Anterior extremity of scutum strongly convex in profile, the largely impunctate, vertical, anterior zone rising well above pronotum and curving onto dorsal surface without sharp line of separation. 11. Pre-episternal groove often short and shallow below scrobal groove. Metanotum not or partly tomentose. 12. Dorsal surface of propodeum longer than metanotum, shorter than to as long as scutellum, striate to granular; triangular area sometimes defined by end of striate or granular zone, broad when recognizable. Lateral and posterior surfaces of propodeum with or without short hairs in addition to long ones, these surfaces not areolate. Posterior surface of propodeum margined by carinae only below, laterally. 13. Apical wing veins strong, recurrent veins entering second and third submarginal cells. 14. Third submarginal cell a little elongate, third transverse cubital arcuate, usually straight toward costal margin of wing, or sinuate. 15. Marginal cell rather robust with free part distinctly less than twice as long as part subtended by submarginal cells, apex pointed very near wing margin or separated from it by about a vein width, not appreciably appendiculate. 16. First metasomal tergum much broader than long. 17. Terga without basal areas or bands of tomentum (very sparse tomentum on tergum II basolaterally in *P. braunsella*). Terga sometimes uniformly sparsely hairy, but more often with hairs denser and more plumose toward posterior margins of terga, often forming strong fasciae of plumose hairs on these margins as in *Halictus*. 18. Apical margins of terga broadly depressed with punctation about as on more anterior parts, hairs not directed laterally or hairs in fasciae weakly so, only very narrow tergal margins impunctate and hairless, these margins or broader areas translucent and pallid. Discs of terga II and III sometimes with oblique hairs.



FIGS. 10-19. Structures of *Patellapis* (*Lomatalictus*). 10-16. *P. malachurina*. 17-19. *P. pallidicinctula*. 10, 11. Dorsal, ventral, and lateral views of male genitalia. 12. Posterior lateral view of male gonostylus. 13. Metasomal sterna VII and VIII of male. 14. Basitibial plate of female. 15. Claw of female. 16, 17. Inner hind tibial spurs of females. 18. Claw of female. 19. Basitibial plate of female.

Male: 19. Clypeus and legs without yellow or white areas. 20. Body of labrum two (in *P. braunsella*) to over three times as wide as long, fringed with bristles, without apical process or with a short triangular process, or in *P. schultzei* with strong, keeled apical process almost like that of a female. Mandible simple or in *Lomatalictus* bidentate. 21. Flagellum short to moderate in length, first segment broader than long, second and sometimes third and fourth broader than long to longer than broad, middle segments usually distinctly longer than broad, sometimes 1.5 times as long as broad. 22. Basitibial plate present or absent. 23. First two hind tarsal segments apparently articulated, but base of second broader than base of third. 24. Metasoma moderately robust, shaped about as in female, third segment widest or second and third equal. 25. Pygidial plate rather large, defined by strong carina both laterally and apically, smooth area longer than broad to slightly broader than long. 26. Sternum IV often short and largely or wholly hidden by III, usually with a series of bristles. Sternum V unmodified to broadly emarginate apically. 27. Sternum VII a transverse band with median apical projection; VIII with broadly rounded, truncate or emarginate apical projection, often with hairs. 28. Genitalia broad with somewhat narrow base (broad base in *P. schultzei*). Gonostylus bifid distally (upper branch sometimes delicate and difficult to see, especially in *P. schultzei*), more than half as long as gonobase, with retrorse, ventral, basal, membranous lobe which is sometimes bifid (e.g., in *P. schonlandi*). Penis valve rather slender to enlarged medially, inferior basal process slender and parallel sided in *P. schultzei* or rounded to obliquely truncate.

Female: 29. Scape reaching at least to anterior margin of anterior ocellus, sometimes as in *P. cincticauda* reaching middle of posterior ocellus. Second flagellar segment broader than long (about as broad as long in *P. montagui*), first and even third and others sometimes also broader than long. 30. Labrum with tapering apical process with keel; body of labrum more than twice as broad as long. 31. Hind tibia and its scopa of usual form. 32. Basitibial plate of moderate size, angular or rounded apically, margin elevated, surface dull or shining, with some hairs. 33. Inner hind tibial spur serrate to pectinate. Hind tibia with two apical spines, sometimes short and mere angles, or posterior one commonly absent, so that there is only one spine. 34. Sternal hairs simple to plumose, of moderate length.

Patellapis belongs to the group of genera with the apical wing venation strong and with the fourth metasomal sternum of males armed with bristles (except in the subgenus *Lomatalictus*) and nearly always shortened. It differs from *Pachyhalictus* by the lack of tomentous basal bands on the terga; the ordinary sculpturing and hind tibial shape and scopa of the female, these features being as in most halictines; the pointed marginal cell; the weakly carinate and nonlamellate dorsolateral pronotal angles; and by the large, well defined pygidial plate of the male with the smooth area usually longer than broad. It differs from *Zonalictus* by the lack of apical, colored tergal bands, the hairy and sometimes fasciate apical tergal margins, the shorter and less fully plumose pubescence of the head and thorax (except for *P. malachurina* and allies which resemble *Zonalictus* in this respect), the shorter and more robust form, etc. It would not have been illogical, however, to include *Zonalictus* as a subgenus of *Patellapis*.

KEY TO THE SUBGENERA OF *Patellapis*

1. Claws of female simple or with inner tooth very small, of male with the teeth close together. Fourth sternum of male similar in size and vestiture to third ..... *Lomatalictus*

.... Claws toothed as usual in halictines. Fourth sternum of male usually shortened, often largely hidden under third,

FIG. 20. Top row: *Patellapis* (*Lomatalictus*) *malachurina,* face of male, face and wing of female. Bottom row: *Patellapis* (*Chaetalictus*) *pearstonensis,* wing and face of female, face of male. Scale line = 1.0 mm.

with a few to many coarse bristles in a transverse row 2

2. Terga with conspicuous apical hair bands; basitibial plate margined both in front and behind, apex in female usually rounded ..... *Patellapis s. str.*

.... Terga without or with weak apical hair bands; basitibial plate not or incompletely defined on anterior margin, apex angulate or pointed .... *Chaetalictus*

The subgeneric classification is not entirely satisfactory. When more species are known from both sexes, it should be reexamined. There is great diversity within the genus and even within the subgenera.

Lomatalictus new subgenus

Figures 10-20

Type species: *Halictus malachurinus* Cockerell, 1937.

Clypeus only weakly convex in profile. *Mandible of male bidentate. Claws of female with small inner tooth or in P. pallidicinctula, simple.* Basitibial plate slender, narrowly rounded or angulate at apex in female, defined only along posterior margin and at apex in male. Inner hind tibial spur of female finely pectinate-serrate (in *P. pallidicinctula*) to pectinate. Metasomal tergal apices broadly pallid translucent with strong apical bands of plumose hairs. *Fourth sternum of male unmodified.* Penis valve without enlarged dorsal crest.

The male of *pallidicinctula* is unknown to me; the above comments on males are based on *P. malachurina.*

Lomatalictus is known only from South Africa. There may be only two species; *P. pallidicinctula* is clearly different from *malachurina,* but the other two names may both be synonyms of the latter.

Included names, all described in *Halictus* and all new combinations, are as follows:

Patellapis (*Lomatalictus*) *levisculpta* (Cockerell, 1939)
Patellapis (*Lomatalictus*) *malachurina* (Cockerell, 1937)
Patellapis (*Lomatalictus*) *pallidicinctula* (Cockerell, 1939)
Patellapis (*Lomatalictus*) *suprafulva* (Cockerell, 1946)

The name *Lomatalictus* is based on *lomatos,* fringes, plus *Halictus,* with reference to the apical bands of hairs on the metasomal terga.

FIGS. 21-25. *Patellapis* (*Chaetalictus*) *pearstonensis.* 21. Fourth sternum of male. 22. Gonocoxite and stylus of male in ventral view. 23. Inner hind tibial spur of female. 24. Claw of female. 25. Gonostylus of male in posterior lateral view.

Chaetalictus new subgenus

Figures 20-26

Type species: *Halictus pearstonensis* Cameron, 1905.

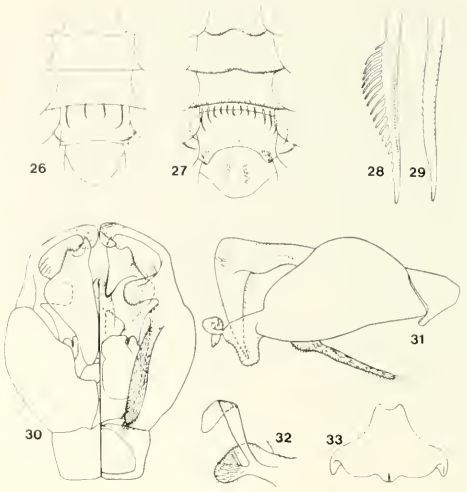
Clypeus markedly convex in profile. Mandible of male simple. Claws normal for halictines. Basitibial plate of female rather slender, weak on anterior margin, narrowly rounded to angulate at apex, as in

Lomatalictus; of male absent to small, undefined anteriorly, with angulate apex. Inner hind tibial spur of female finely pectinate-serrate (in *P. serifera,* as figured for *P. pallidicinctula*) to pectinate. Metasomal terga with translucent margins narrow to broad, apical hair bands weak or absent. Sternum IV of male of normal size to shortened, broadly emarginate, and hidden under III; it bears six enormous bristles or (in *P. rubrotibialis*) a row of often erect or retrorse bristles, only the lateral ones of which are large, or (in *P. pulchrinitens*) a row of rather weak bristles. Penis valve without enlarged dorsal crest.

This subgenus, known only from southern Africa, consists of species mostly smaller than those of *Patellapis s. str.*

Included names, all described in *Halictus* and all new combinations, are as follows:

Patellapis (*Chaetalictus*) *atricilla* (Cockerell, 1940)
Patellapis (*Chaetalictus*) *ausica* (Cockerell, 1945)
Patellapis (*Chaetalictus*) *calvini* (Cockerell, 1937)
Patellapis (*Chaetalictus*) *calviniensis* (Cockerell, 1934)
Patellapis (*Chaetalictus*) *capillipalpus* (Cockerell, 1946)
Patellapis (*Chaetalictus*) *chubbi* (Cockerell, 1937)
Patellapis (*Chaetalictus*) *cinctifera* (Cockerell, 1946)
Patellapis (*Chaetalictus*) *communis* (Smith, 1879)
Patellapis (*Chaetalictus*) *disposita* (Cameron, 1905)
Patellapis (*Chaetalictus*) *dispositina* (Cockerell, 1934)
Patellapis (*Chaetalictus*) *flavorufa* (Cockerell, 1937)
Patellapis (*Chaetalictus*) *leonis* (Cockerell, 1940)
Patellapis (*Chaetalictus*) *micropastina* (Cockerell, 1940)
Patellapis (*Chaetalictus*) *neli* (Cockerell, 1937)
Patellapis (*Chaetalictus*) *pastina* (Cockerell, 1937)

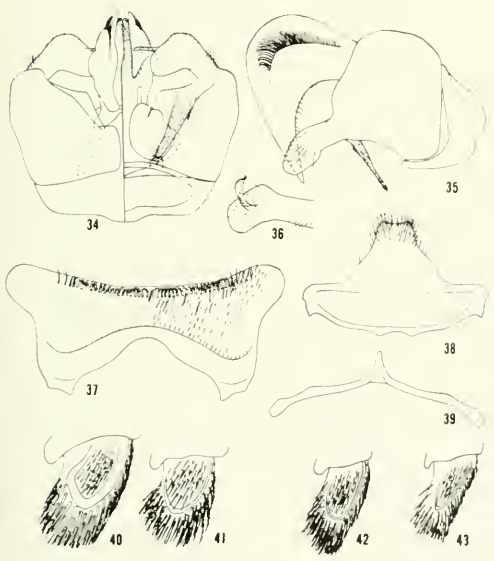


FIGS. 26-33. Structures of *Patellapis.* 26, 27. Metasomal sterna of males, with sparse hairs omitted, but areas of dense pubescence shown, of *P.* (*Chaetalictus*) *pearstonensis* and *P.* (*Patellapis*) *braunsella.* 28, 29. Inner hind tibial spurs of females, *P.* (*P.*) *montagui* and *braunsella.* 30, 31. Dorsal, ventral and lateral views of male genitalia, *P.* (*P.*) *braunsella.* 32. Posterior lateral view of male gonostylus of same. 33. Eighth sternum of same.

Patellapis (*Chaetalictus*) *pastinella* (Cockerell, 1939)
Patellapis (*Chaetalictus*) *pastiniformis* (Cockerell, 1939)
Patellapis (*Chaetalictus*) *pearstonensis* (Cameron, 1905)
Patellapis (*Chaetalictus*) *pondoensis* (Cockerell, 1937)
Patellapis (*Chaetalictus*) *probita* (Cockerell, 1933)
Patellapis (*Chaetalictus*) *pulchrinitens* (Cockerell, 1937)
Patellapis (*Chaetalictus*) *rubrotibialis* (Cockerell, 1946)
Patellapis (*Chaetalictus*) *rufiventris* (Friese, 1925) (not *Halictus rufiventris* Giraud, 1861)
Presumably a synonym of *pearstonensis* and hence not in need of a new name.
Patellapis (*Chaetalictus*) *sanguinibasis* (Cockerell, 1939)

Patellapis (*Chaetalictus*) *schonlandi* (Cameron, 1905)
Patellapis (*Chaetalictus*) *semipastina* (Cockerell, 1940)
Patellapis (*Chaetalictus*) *serrifera* (Cockerell, 1937)
Patellapis (*Chaetalictus*) *spinulosa* (Cockerell, 1941)
Patellapis (*Chaetalictus*) *tenuihirta* (Cockerell, 1939)
Patellapis (*Chaetalictus*) *terminalis* (Smith, 1853)
Patellapis (*Chaetalictus*) *vambensis* (Cockerell, 1940)
Patellapis (*Chaetalictus*) *villosicauda* (Cockerell, 1937)
Patellapis (*Chaetalictus*) *volutatoria* (Cameron, 1905)

The name *Chaetalictus* is based on *chaetes,* bristle or hair, plus *Halictus,* with reference to the coarse bristles on the fourth sternum of the males.



Figs. 34-43. Structures of *Patellapis* (*Patellapis*). 34, 35. Dorsal, ventral and lateral views of male genitalia of *Patellapis* (*P.*) *schultzei.* 36. Posterior lateral view of gonostylus of same. 37-39. Fourth, eighth, and seventh sterna of same. 40, 41. Basitibial plates of female and male, *P.* (*P.*) *schultzei.* 42, 43. Basitibial plates of female and male, *P.* (*P.*) *braunsella.*

Subgenus *Patellapis* Friese, s. str.

Figures 27-44

Patellapis Friese, 1909, Die Bienen Afrikas, p. 148, *in* L. Schultze, Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Südafrika, vol. 2, part 2.

Type species: *Halictus* (*Patellapis*) *schultzei* Friese, by designation of Cockerell, 1920, Ann. Durban Mus., 2:311.

Agrees with description of *Chaetalictus* except as follows: Mandible of male simple or in *minutior* bidentate. Basitibial plate of female rather broad, margin well defined throughout, not weak on anterior side, apex rounded or weakly angulate; of male similarly broad and well defined in *P. schultzei,* narrower, pointed apically, but defined by carina at least part way up anterior margin in other species. Inner hind tibial spur of female weakly serrate to pectinate. Metasomal terga with broad translucent pallid margins and strong apical bands of plumose hair. Sternum IV of male unmodified in shape (in *P. "minutior"*) to shortened, broadly concave apically, and largely hidden by III, in all species with a transverse row of coarse bristles, the lateral ones greatly enlarged in *P. braunsella,* but not in others. Penis valve with median dorsal carina greatly expanded to form apically directed helmet-like crest.

This subgenus, known only from Cape Province, South Africa, contains the following species:

Patellapis (*Patellapis*) *braunsella* new species
Patellapis (*Patellapis*) *cincticauda* (Cockerell, 1946) new comb.
Patellapis (*Patellapis*) *minutior* (Friese, 1909)
Patellapis (*Patellapis*) *montagui* (Cockerell, 1941) new comb.
Patellapis (*Patellapis*) *schultzei* (Friese, 1909)

The specimen of *P. minutior* used for this study was labeled "typus" by Friese and is in the American Museum of Natural History. Other specimens, similarly labeled, in the Berlin museum are a different species of the same subgenus, with simple mandibles and other features not agreeing with my comments on *minutior.* Presumably the Berlin specimens are the true *minutior.* I have therefore placed the name in quotes where reference is to the

FIG. 44. Top row: *Patellapis* (*Patellapis*) *schultzei*, face of male and *P.* (*P.*) *montagui*, face and wing of female. Middle row: *Patellapis* (*P.*) *braunsella*, face of male, face and wing of female. Bottom row: *Zonalictus albofasciatus*, face of male, face and wing of female. Scale line = 1.0 mm.

specimen in the American Museum. It does not seem to me appropriate to name the species at present, since I have seen only a single specimen in poor condition.

P. cincticauda is placed in this subgenus hesitantly, since I have seen no males and have not examined specimens since recognizing the limits of this group. The genitalia of *P. schultzei* and *P. braunsella* are quite different as illustrated, but those of *P. "minutior"* are intermediate in gonobase width and some other features.

Great diversity within as well as between the subgenera of *Patellapis* sometimes confuses the subgeneric limits. The bristles of the fourth sternum of the male in *P. braunsella* are greatly enlarged laterally, suggesting *P.* (*Chaetalictus*) *rubrotibialis*. The size and shape of the same sternum (not shortened) in *P. "minutior"* suggest *Lomatalictus,* as do the bidentate mandibles of the male. The one female specimen of a minute and presumably undescribed species of *Chaetalictus* has claws with only a small inner tooth, like those of *P.* (*Lomatalictus*) *malachurina*. There are very striking differences among species of at least the genera *Patellapis* and *Chaetalictus,* and the subgenera here recognized may be inadequate to properly reflect this diversity, or the limits of the subgenera recognized may not be ideal. One of the major problems is that for too many species only one sex is known, so that the full suite of specific characters is not available. The classification presented above is, therefore, tentative and conservative in that few subgenera are named. When both sexes are known for most of the species, more subgenera may be desirable.

Zonalictus new genus

Figures 44-53

Halictus albofasciatus-Gruppe, Blüthgen, 1929, Mitt. Zool. Mus. Berlin, 15:29.

Type species: *Halictus albofasciatus* Smith.

1. Nonmetallic black (sometimes with a partly red metasoma), usually with white, yellow, greenish, or bluish apical, integumental bands on terga; 6.5-14 mm long. 2. Surface of head and thorax commonly dull; frons and usually dorsum of thorax finely reticulate, the latter sometimes with punctures of two sizes intermixed, rarely shining with scattered punctures. *Pubescence long, plumose, commonly yellowish,* there being almost no areas of short, whitish, pubescence or tomentum as in most halictine groups [but *Patellapis* (*Lomatalictus*) *malachurina* and its relatives are similar in this respect]. 3. Clypeus neither produced downward nor protuberant forward (except strongly produced downward in the long-headed species *Z. zacephalus*), two to three times as broad as long, angle at end of truncation not or feebly produced, surface sometimes shining, but usually dull basally, large punctures often limited to distal half of clypeus; clypeal profile sometimes uniformly convex, but usually flat basally and strongly convex distally. 4. Line between lower ends of eyes crossing clypeus below or above middle. 5. Malar space linear. 6. Paraocular area not extending down as lobe into clypeus, or forming an obtuse lobe or angle. Mouthparts short and ordinary or in *Z. zacephalus,* glossa over half as long as face, in *Z. concinnulus* glossa longer than face and first two segments of labial palpus much elongated. 8. Pronotum with dorsal surface medially not defined, sloping anteriorly, but elsewhere defined anteriorly by declivity of pronotal surface, not by carina; dorsal surface (collar) often weakly tomentose. 9. Dorsolateral angle of pronotum obtuse, not lamellate or carinate, a ridge (often weak) extending laterally in some species across pronotal lobe, a rounded or sometimes sharp ridge extending downward from dorsolateral angle. 10. Anterior extremity of scutum as described for *Patellapis*. Preepisternal groove as described for *Patellapis*. Metanotum not or scarcely tomentose. 12. Dorsal surface of propodeum usually as long as scutellum, sometimes slightly shorter, finely granular or granulostriate; triangular area sometimes defined by weak carinae, usually not defined, when recognizable, broad. Lateral and posterior surfaces of propodeum without short hairs in addition to long ones, not areolate. Posterior surface margined by carinae only below laterally. 13. Wing venation as in *Patellapis,* but marginal cell more slender. 16. First metasomal tergum broader than long or in some males longer than broad. 17. Terga without basal areas or bands of tomentum (rarely very feeble tomentum basolaterally on tergum II, as in *Z. albofilosus*), without apical hair bands, hairs smaller and commonly sparser on apical parts of terga 1-4 than elsewhere, *these margins usually highly colored, at least on tergum 1, forming white, yellow, greenish, or bluish integumental bands.* 18. Apical margins of terga broadly and weakly depressed, not punctate, but with hairs similar to but smaller than those on rest of terga, hairs not directed laterally; margins of terga hairless, not translucent when highly colored, but broadly

FIGS. 45-53. Structures of *Zonalictus*. 45, 46. Dorsal, ventral and lateral views of male genitalia of *Z. albofasciatus*. 47. Posterior lateral view of stylus of same. 48. Seventh tergum of same. 49. Fourth sternum of same. 50-52. Inner hind tibial spurs of females of *Z. partitus, albofasciatus,* and *zacephalus*. 53. Ventral view of male gonocoxite and gonostylus of *Z. cinctulellus*.

translucent when not colored. Discs of terga II and III without oblique hairs.

Male: 19. Clypeus often with apical transverse yellow area; labrum often partly yellow; legs without yellow. 20. Labrum usually over three times as wide as long, without or with a barely evident apical process, but in *Z. concinnulus* only about twice as wide as long because of a strong, triangular apical process (not keeled). Mandible simple (bidentate in *Z. concinnulus*). 21. Flagellum elongate, first segment a little broader than long, other segments much longer than broad. 22. Basitibial plate present and well defined to nearly absent with only the apex distinct. 23. First two hind tarsal segments articulated as in *Patellapis*. Metasoma rather elongate, widest at segments 2 and 3. 25. Pygidial plate moderately large, defined by a strong carina both laterally and apically, smooth area usually longer than broad. 26. Sternum IV shortened, largely hidden by III, sometimes with a series of coarse bristles becoming progressively larger laterally (as in *Patellapis braunsella*), but usually with a series of erect or retrorse bristles of uniform size medially and one enormous, isolated, largely hidden, lateral bristle at each side. 27. Sternum VII a transverse band with median apical projection; VIII with produced apex emarginate. 28. Genitalia broad with somewhat narrow base. Gonostylus bifid distally, more than half as long as gonobase, with retrorse, ventral, basal, membranous lobe which may be large and bifid or may be much reduced in size. Penis valve rather slender, dorsal keel not expanded as in *Patellapis s. str.*, inferior basal process broadly rounded or subtruncate at apex.

Female: 29. Scape reaching posterior ocellus. Second flagellar segment as long as broad or usually broader than long, others commonly longer than broad, but mostly broader than long in some species (e.g., *Z. zacephalus*). 30. Labrum with tapering or sometimes rounded apical process with keel, body of labrum more than twice as broad as long. 31. Hind tibia and its scopa of the usual form. 32. Basitibial plate of moderate size, angular or narrowly rounded apically, margin elevated throughout or anterior margin largely absent so that plate is defined only apically and posteriorly; surface of plate with some hairs. 33. Inner hind tibial spur usually coarsely serrate to pectinate with short teeth, but in *Z. zacephalus* finely ciliate-serrate. Hind tibia with one tibial spine. 34. Sternal hairs short to moderate in length, simple to plumose, not suggestive of a scopa.

Zonalictus is closely related to *Patellapis* and could easily be incorporated into that genus as a subgenus. Because of its rather elongate form, the long, yellowish plumose hairs, and the integumental color bands on the apices of the metasomal terga (very rarely absent but often limited to tergum I or I and II), it has a different appearance from *Patellapis* or other halictids. Because of this fact, and other characters which are not invariable, such as the yellow on the clypeus of the male, the usually longer male antennae, and the commonly dull integumental surfaces between punctures, I have hesitantly accorded *Zonalictus* generic status.

Zonalictus is found throughout subsaharan Africa and eastward to Madagascar, Socotra, and Yemen. The specific names known to be included are listed below. Names preceded by an asterisk are placed here on the basis of literature only.

Zonalictus aberdaricus (Cockerell, 1945)
**Zonalictus abessinicus* (Friese, 1916)
Zonalictus albofasciatus (Smith, 1879)
Zonalictus albofilosus (Cockerell, 1937)
Zonalictus albolineolus (Meade-Waldo, 1916)
Zonalictus alopex (Cockerell, 1937)
Zonalictus andersoni (Cockerell, 1945)
**Zonalictus andreniformis* (Friese, 1925)
**Zonalictus andrenoides* (Friese, 1909)

Zonalictus baralongus (Cockerell, 1939)
**Zonalictus bilineatus* (Friese, 1909)
Zonalictus broomi (Meade-Waldo, 1916), *nomen nudum*
Zonalictus burunganus (Cockerell, 1937)
**Zonalictus burungensis* (Cockerell, 1937)
Zonalictus cerealis (Cockerell, 1945)
Zonalictus cinctulellus (Cockerell, 1946)
Zonalictus concinnulus (Cockerell, 1946)
**Zonalictus flavofasciatus* (Friese, 1915)
Zonalictus flavovittatus (Kirby, 1900)
Zonalictus fuliginosus (Cockerell, 1937)
Zonalictus gowdeyi (Cockerell, 1937)
Zonalictus grandior (Blüthgen, 1929)
Zonalictus hargreavesi (Cockerell, 1946)
Zonalictus heterozonicus (Cockerell, 1937)
Zonalictus kabetensis (Cockerell, 1937)
**Zonalictus kamerunensis* (Friese, 1914) (This is the first of two forms to which Friese gave the same trivial name on the same page.)
Zonalictus kavirondicus (Cockerell, 1945)
Zonalictus kivuicola (Cockerell, 1937)
Zonalictus knysnae (Cockerell, 1945)
Zonalictus kristenseni (Friese, 1915)
Zonalictus macrozonius (Cockerell, 1937)
Zonalictus microzonius (Cockerell, 1937)
Zonalictus minor Blüthgen, 1929 (not *Halictus minor* Morawitz, 1876) (Named as a variety of *andreniformis;* no replacement name seems needed.)
Zonalictus mirandicornis (Cockerell, 1939)
Zonalictus moshiensis (Cockerell, 1937)
Zonalictus neavei (Cockerell, 1946)
Zonalictus nefasiticus (Cockerell, 1935)
Zonalictus nomioides (Friese, 1909)
Zonalictus pallidicinctus (Cockerell, 1933)
Zonalictus partitus (Cockerell, 1933)
Zonalictus patriciformis (Cockerell, 1933)
Zonalictus pearsoni (Cockerell, 1933)
Zonalictus percinctus (Cockerell, 1937)
Zonalictus perlucens (Cockerell, 1933)
Zonalictus perpansus (Cockerell, 1933)
Zonalictus promitus (Cockerell, 1934)
Zonalictus pulchricinctus (Cockerell, 1933)
Zonalictus pulchrihirtus (Cockerell, 1933)
**Zonalictus rufobasalis* (Alfken, 1930)
Zonalictus ruwensorensis (Strand, 1911)
Zonalictus sidulus (Cockerell, 1937)
Zonalictus stanleyi (Cockerell, 1945)
**Zonalictus subpatricius* Strand, 1911
Zonalictus subvittatus (Cockerell, 1937)
Zonalictus tenuimarginatus (Friese, 1925)
Zonalictus territus (Cockerell, 1937)
Zonalictus tinctulus (Cockerell, 1937)
Zonalictus tricolor (Meade-Waldo, 1916, *nomen nudum,* not *Halictus tricolor* Lepeletier, 1841
Zonalictus trifilosus (Cockerell, 1945)
Zonalictus unifasciatus (Cockerell, 1937)
Zonalictus viridifilosus (Cockerell, 1946)
Zonalictus vittatus (Smith, 1853)
**Zonalictus weisi* (Friese, 1915)
Zonalictus zacephalus (Cockerell, 1937)
Zonalictus zaleucus (Cockerell, 1937)

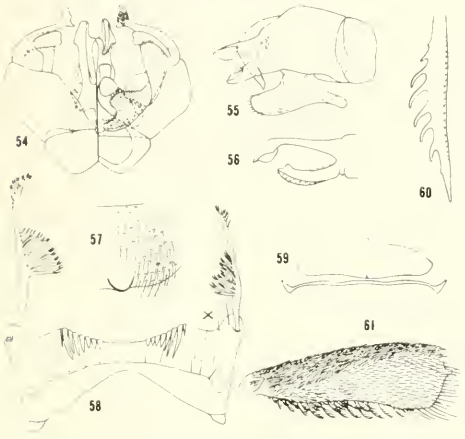
The name *Zonalictus* is based on *zone,* a belt or girdle, plus *Halictus,* with reference to the conspicuous integumental metasomal color bands of many species.

Genus *Pachyhalictus* Cockerell

Figures 54-68

1. Nonmetallic black, rather small, robust, 5.5-7 mm long. 2. *Frons, scutum and scutellum reticulate*

(more finely on frons), not punctate, or occasionally partly smooth or, as in *P. binghami,* with fine wrinkles and shallow punctures. 3. Clypeus neither produced downward nor protuberant forward, about three times as wide as long or wider, angle at end of truncation not or feebly produced, surface closely punctured or reticulate and dull, uniformly gently convex. 4. Line between lower ends of eyes crossing clypeus below or above middle. 5. Malar space linear. 6. Paraocular area not extending down as lobe into clypeus, lateral clypeal margins only weakly curved and at an obtuse angle to one another. 7. Mouthparts short, the short glossa exceeded by labial palpi, postpalpal part of galea not much longer than broad.



FIGS. 54-61. Structures of *Pachyhalictus* (*Pachyhalictus*). 54, 55. Dorsal, ventral, and lateral views of male genitalia of *P.* (*P.*) species γ of Blüthgen, 1926. 56. Posterior lateral view of gonostylus of same. 57. Median part of seventh tergum of same. 58. Fourth sternum of same, with detached giant seta in different view (X indicates a damaged area, reconstructed in drawing). 59. Seventh and eighth sterna of same. 60. Inner hind tibial spur of female of *P.* (*P.*) *meresceens.* 61. Outer surface of hind tibia of same.

8. Pronotum with horizontal dorsal surface medially one half (in *P. retigerus*) to one third as long as flagellar width, often densely tomentose, margined anteriorly in middle only by sharp declivity of pronotal surface, but laterally by carina or lamella. 9. Dorsolateral angle of pronotum obtuse, but formed by strong anteriorly or upward directed carina or lamella which extends across posterior pronotal lobe. 10. Anterior extremity of scutum sharply angular in profile, the largely impunctate vertical or overhanging anterior zone rising well above pronotum and sometimes separated from rest of scutal surface by a carina. 11. Preepisternal groove well developed. *Metaplura strongly narrowed below,* where narrowest less than one third as wide as at upper end. Metanotum tomentose. 12. Dorsal surface of propodeum slightly shorter than to longer than scutellum, usually coarsely areolate, sometimes irregularly coarsely striate, intervals or areolae dull or in *P. retigerus* shining. Triangular area not or scarcely defined. Lateral and posterior propodeal surfaces with short hairs in addition to long ones, these surfaces usually areolate. Posterior surface of propodeum usually margined all the way around by carinae, but *P. binghami* and *retigerus* without carina across summit or on upper parts of sides. 13. Apical wing veins strong. Recurrent veins entering second and third submarginal cells near apices, first sometimes almost interstitial; in *P. retigerus* both recurrents entering cells at apical third or fourth. (One specimen seen lacking first transverse cubital, another lacking second; species with only two submarginal cells may exist.) 14. Third submarginal cell short, third transverse cubital vein straight or arcuate, not sinuate or in *P. retigerus* feebly so. 15. Stigma of moderate size. Marginal cell with free part less than twice as long as part subtended by submarginal cells, apex appendiculate, minutely truncate to pointed, apex separated from wing margin by less than to more than two vein widths. 16. First metasomal tergum much broader than long. 17. Terga II, III, and sometimes IV with strong basal bands of pale tomentum, without apical fasciae. 18. Apical margins of terga broadly, weakly depressed with hairs and punctation usually about as on more anterior parts of same terga; hairs not or scarcely directed laterally; only very narrow tergal margins impunctate, pallid, and hairless (broad marginal zones impunctate when discs of terga are also largely impunctate as for terga I and II of *P. retigerus*). Discs of terga II and III sometimes with oblique hairs.

Male: 19. Clypeus and legs without yellow or white areas. 20. Labrum nearly or over four times as wide as long, fringed with bristles, without apical process. Mandible simple. 21. Flagellum short, all but last two or three segments broader than long or middle segments about as broad as long, first segment much broader than long. 22. Basitibial plate absent (present in *P. retigerus*). 23. First two hind tarsal segments distinct or fused, but point of union indicated by strong constriction. 24. Metasoma robust, shaped about as in female. 25. Pygidial plate small, defined by carina which curves forward laterally, so that it margins the plate both laterally and apically. 26. Sternum IV broadly emarginate posteriorly, median part much shortened, hidden by III, thickened, with an apical series of erect bristles on each side of midline (Blüthgen's species γ) and often with an enormous lateral bristle (sometimes hooked as in *bihamatus*) (armature of sternum IV probably highly variable among species, bristles sometimes entirely hidden by sternum III). Sternum V gently emarginate apically (at least in species γ and *P. retigerus*). 27. Sterna VII and VIII much reduced, membranous, VII a slender transverse strip in species γ, with small median apical projection in *P. retigerus,* VIII damaged, but apparently hairless and without significant apical projection. 28. Genitalia broad with somewhat narrow gonobase; gonostylus ornate, main part deeply bifid, as long as gonobase; retrorse, membranous,

basal lobe itself bilobed, one part extending distad, the other mesad. Penis valve slender, inferior basal process subtruncate (based on Blüthgen's species γ and on *P. retigerus*).

Female: 29. Scape reaching or nearly reaching anterior margin of anterior ocellus. Second, often first, and sometimes other flagellar segments broader than long. 30. Labrum with tapering apical process with keel, body of labrum much more than twice as wide as long. 31. Hind tibia rather robust, lower surface and therefore lower margin as seen from side gently concave, scarcely so in *P. retigerus,* outer surface largely covered with rather short, nearly erect hairs of uniform length, upper surface with short bristles; lower margin on outer surface with long, coarse, hairs, especially those of basal half of the tibia with more numerous, crowded, and coarser branches than in most halictids, all directed toward apex of tibia. 32. Basitibial plate of moderate size, triangular to rounded apically, margin elevated, surface dull, shining in *P. retigerus,* with some hairs. 33. Inner hind tibial spur pectinate with a few coarse to many fine teeth. Hind tibia without or with one short tibial spine. 34. Sterna and ventral parts of terga with plumose hairs which in some Indoaustralian species are large, richly plumose, and important scopal structures.

Pachyhalictus resembles *Homalictus* in the peculiar shape and vestiture of the hind tibia of the female and some species even have such a large ventral metasomal scopa as to suggest *Homalictus.* In many ways, however, *Pachyhalictus* differs from *Homalictus,* e.g., the robust body, basal bands of tomentum on the terga, and strong second recurrent and third transverse cubital veins. In this feature of venation and in the shortened, largely hidden fourth metasomal sternum of the male, *Pachyhalictus* resembles *Patellapis,* from which it differs in the structure of the tibia of the female, basal bands of tomentum, etc. The bifid gonostyli also suggest a relationship to *Patellapis.* The distinctive reticulate sculpturing of *Pachyhalictus* is found in a very few species of *Patellapis* and *Zonalictus.*

Pachyhalictus is found principally from the Asiatic tropics and nearby islands to New Guinea. One species (*P. stirlingi*), however, occurs in northern Australia. Another, *P. retigerus,* morphologically differentiated but clearly a member of the genus, occurs in southeastern Africa.

Key to the Subgenera of *Pachyhalictus*

1. Inner hind tibial spur of female coarsely pectinate with three to six long teeth; basitibial plate of male absent or nearly so; first two hind tarsal segments of male fused ..... *Pachyhalictus s. str.*

.... Inner hind tibial spur of female finely pectinate with more than 12 slender teeth; basitibial plate of male present; first two hind tarsal segments of male articulated ..... *Dictyohalictus*

Subgenus *Pachyhalictus* Cockerell, s. str.

Figures 54-61

Halicti nomiiformes Vachal, 1894, Ann. Mus. Civ. Genova, 34:428 (part); Blüthgen, 1926, Zool. Jahrb., Abt. Syst., Geogr. Biol. Tiere, 51:400; Blüthgen, 1931, Zool. Jahrb., Abt. Syst., Geogr. Biol. Tiere, 61:286.

Pachyhalictus Cockerell, 1929, Ann. Mag. Nat. Hist., (10)4:589. Type species: *Halictus merescens* Cockerell, 1919, original designation.

Recurrent veins entering second and third submarginal cells near apices or the first interstitial. Third transverse cubital vein arcuate or nearly straight. Basitibial plate of male absent or indicated only apically. First two hind tarsal segments of male fused, but point of union indicated by strong constriction. Fourth sternum of male with an enormous lateral bristle hidden by the tergum, at least in species that have been dissected. Inner hind tibial spur of female pectinate with three to six long, coarse teeth.

Pachyhalictus s. str. is restricted to the Indoaustralian region, ranging from Ceylon and India eastward to the Philippines and Taiwan and through Indonesia, New Guinea, to northern Australia. The following is a list of species names, all new combinations in *Pachyhalictus,* based on Blüthgen (1926, 1928, 1931) plus my examinations of type material. Synonymies are those of Blüthgen, not re-evaluated here.

Pachyhalictus (*Pachyhalictus*) *assamicus* (Blüthgen, 1926)
Pachyhalictus (*Pachyhalictus*) *bedanus* (Blüthgen, 1926)
**Pachyhalictus* (*Pachyhalictus*) *bihamatus* (Blüthgen, 1926)
Pachyhalictus (*Pachyhalictus*) *binghami* (Kirby, 1900)

Pachyhalictus (*Pachyhalictus*) *burmanus* (Blüthgen, 1926)
Pachyhalictus (*Pachyhalictus*) *buruanus* (Blüthgen, 1926)
Pachyhalictus (*Pachyhalictus*) *celebensis* (Blüthgen, 1931)
Pachyhalictus (*Pachyhalictus*) *dapanensis* (Blüthgen, 1926)
Pachyhalictus (*Pachyhalictus*) *formosicola* (Blüthgen, 1926)
**Pachyhalictus* (*Pachyhalictus*) *interstitialis* (Cameron, 1903)
**Pachyhalictus* (*Pachyhalictus*) *intricatus* (Vachal, 1894) (=*thoracicus* Friese, 1914)
Pachyhalictus (*Pachyhalictus*) *javanus* (Blüthgen, 1926)
**Pachyhalictus* (*Pachyhalictus*) *kalutarae* (Cockerell, 1911) (=*amplicollis* Friese, 1918)
Pachyhalictus (*Pachyhalictus*) *kocki* (Blüthgen, 1931)
**Pachyhalictus* (*Pachyhalictus*) *liodomus* (Vachal, 1894) =*scopipes* Friese, 1918)
Pachyhalictus (*Pachyhalictus*) *lombokensis* (Blüthgen, 1926)
Pachyhalictus (*Pachyhalictus*) *merescens* (Cockerell, 1919)
Pachyhalictus (*Pachyhalictus*) *murbanus* (Blüthgen, 1931)
Pachyhalictus (*Pachyhalictus*) *negriticus* (Blüthgen, 1926)
Pachyhalictus (*Pachyhalictus*) *penangensis* (Blüthgen, 1926)
Pachyhalictus (*Pachyhalictus*) *pseudothoracicus* (Blüthgen, 1926)
Pachyhalictus (*Pachyhalictus*) *puangensis* (Cockerell, 1937)
**Pachyhalictus* (*Pachyhalictus*) *reticulosus* (Dalla Torre, 1896) (=*Halictus reticulatus* Vachal, 1894, not Robertson, 1892)
**Pachyhalictus* (*Pachyhalictus*) *sigiriellus* (Cockerell, 1911)
Pachyhalictus (*Pachyhalictus*) *stirlingi* (Cockerell, 1910)
**Pachyhalictus* (*Pachyhalictus*) *sublustrans* (Cockerell, 1919)
Pachyhalictus (*Pachyhalictus*) *trizonulus* (Friese, 1909)
**Pachyhalictus* (*Pachyhalictus*) *validus* (Bingham, 1903)
Pachyhalictus (*Pachyhalictus*) *vanajus* (Blüthgen, 1926)
**Pachyhalictus* (*Pachyhalictus*) *vinctus* (Walker, 1860)

Of these species, *P. binghami* from Christmas Island in the Indian Ocean, is most distinctive, differing from ordinary *Pachyhalictus* in the less prominent reticulate pattern on the head and thorax (scutum has shallow punctures and fine wrinkles, thus intermediate between punctate and reticulate), and in the propodeal surface pattern (dorsal surface not areolate, with fine longitudinal wrinkles between which surface is dull; carinae margining posterior surface reaching only three fourths of distance to upper margin of that surface).

Dictyohalictus new subgenus

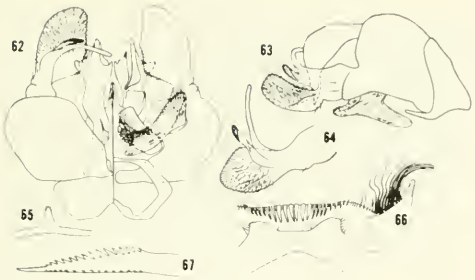
Figures 62-68

Type species: *Halictus retigerus* Cockerell, 1940.

Recurrent veins entering second and third submarginal cells well before apices. Third transverse cubital vein slightly sinuate. Basitibial plate of male present. First two hind tarsal segments of male distinct, although articulation broader than that between second and third segments. Fourth sternum of male with a slender, posteriorly directed lobe at each side, hidden by the tergum, but without a lateral bristle. Inner hind tibial spur of female finely pectinate with more than a dozen rather short, slender teeth.

This subgenus is known only from southeastern Africa. It appears to contain only a single species, *Pachyhalictus* (*Dictyohalictus*) *retigerus* (Cockerell), new combination, but there are several synonyms as indicated in the Appendix.

The name *Dictyohalictus* is based on *diktyon,* a net, plus *Halictus,* with reference to the reticulate sculpturing of the head and thorax.



FIGS. 62-67. *Pachyhalictus* (*Dictyohalictus*) *retigerus*. 62, 63. Dorsal, ventral and lateral views of male genitalia. 64. Posterior dorsal view of male gonostylus. 65. Median part of seventh sternum of male. 66. Fourth sternum of male. 67. Inner hind tibial spur of female.

FIG. 68. Face and wing of female of *Pachyhalictus* (*Dictyohalictus*) *retigerus*. Scale line = 1.0 mm.

Genus *Thrincohalictus* Blüthgen

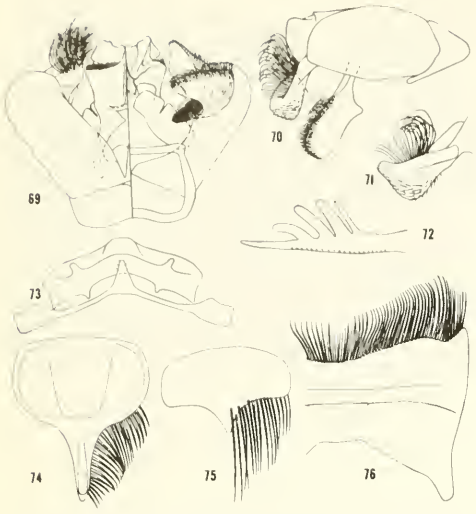
Figures 69-77

Thrincohalictus Blüthgen, 1955, Bull. Research Council Israel (B, Biol., Geol.), 5:20.

Type species: *Halictus prognathus* Pérez, 1912, by original designation and monotypy.

1. Nonmetallic black, moderately robust, length 9-10 mm. 2. Punctation of the usual sort, rather fine and dense. 3. *Clypeus strongly produced downward and protuberant forward,* almost twice as broad as long (female) to little broader than long (male), with shining but roughened ground between irregular punctures, upper part flat in profile; angle at end of truncation weakly produced and rounded or absent in male. 4. Line between lower ends of eyes crossing above middle of clypeus (female) or entirely above clypeus (male). 5. *Malar area conspicuous,* about half as long as basal mandibular width (female) to longer than basal mandibular width (male). 6. Paraocular area extending down as strong lobe into clypeus. 7. Mouthparts long and slender, glossa linear and much exceeding palpi and galea, but galea elongate, postpalpal part about four times as long as wide, and labial palpus about half as long as glossa. 8. Pronotum with horizontal, dorsal surface less than one half as long medially as flagellar width, tomentose, margined anteriorly by angle where pronotal surface becomes declivous. 9. Dorsolateral angle of pronotum obtuse, a rounded ridge, but no carina extending downward from it. 10. Anterior extremity of scutum strongly convex in profile, the largely impunctate, vertical, anterior zone rising well above pronotum and curving uninterruptedly onto dorsal surface. 11. Preepisternal groove well developed. Metanotum tomentose anteriorly. 12. Dorsal surface of propodeum about as long as metanotum, triangular area ill-defined and rather finely areolate or striate. Area behind triangle and lateral and posterior propodeal surfaces with few short hairs in addition to long ones. Posterior and lateral surfaces of propodeum not areolate, separated by carinae only below. 13. Apical wing veins strong. Recurrent veins entering second and third submarginal cells at distal third or fourth. 14. Third submarginal cell somewhat elongate, third transverse cubital vein distinctly sinuate, being arcuate toward wing apex posteriorly and toward wing base anteriorly. 15. Stigma of moderate size. Marginal cell of the usual shape, free part much less than twice as long as part subtended by marginal cells, apex pointed, separated from wing margin by about a vein width or less. 16. First metasomal tergum broader than long. 17. Basal tergal tomentum absent or nearly so. 18. Terga with apical bands of pale plumose hair as in *Halictus*. Tergal margins broadly depressed, with punctation finer than on discs of terga, both hairs and punctures ending before margins proper, which are smooth and bare; hairs of marginal bands not or scarcely directed laterally; integument of marginal bands translucent brownish.

Male: 19. Apex of clypeus and areas on femora, tibiae, and tarsi yellowish white. 20. Labrum slightly over twice as wide as long, with small apical process; long bristles scattered over marginal part of process, not limited to marginal row; no keel. Mandible simple. 21. Flagellum elongate, segments over 1.5 times as long as wide except for first which is wider than long. 22. Basitibial plate absent. 23. First two hind tarsal segments articulated, base of second not or scarcely broader than base of third. 24. Metasoma rather robust, but nearly parallel sided, segments II and III widest. 25. *Pygidial plate not defined by carina, its position occupied by a median projection or tubercle* which has hairs like those of adjacent areas, but above which is an ill-defined bare area. 26. Sternum IV shorter than adjacent sterna and largely hidden, its posterior margin fringed with long, curved bristles directed posteriorly, lateral part without a special elongate lobe or bristle. Sternum V with apical margin broadly and strongly emarginate, extreme side with a pencile of extremely long, curved, apparently fused hairs hidden under sides of terga.



FIGS. 69-76. *Thrincohalictus prognathus*. 69-70. Dorsal, ventral and lateral views of male genitalia. 71. Posterior lateral view of male gonostylus. 72. Inner hind tibial spur of female. 73. Seventh and eighth sterna of male. 74, 75. Labrum of female and male. 76. Fourth sternum of male.

27. Sternum VII a slender transverse bar with a median apical pointed process. Sternum VIII a transverse band, somewhat broadened and sclerotized medially. 28. Genitalia rather broad with narrowed base. Gonostylus rather simple, little over half length of gonocoxite, with large dense tuft of hairs near inner margin, with large, hairy "retrorse" ventral lobe which, however, is largely directed ventro distally, but with small arm directed mesobasally. Penis valve with inferior basal process broadly rounded apically.

Female: 29. Scape reaching to middle of anterior ocellus. First flagellar segment slightly longer than wide. 30. Labrum with keeled apical process narrow; *body of labrum rounded apically, about 1.3 times as wide as long.* 31. Hind tibia and scopa of the usual form. 32. Basitibial plate rather large, about one fourth as long as tibia, distinctly margined, surface largely hairy. 33. Inner hind tibial spur pectinate with four or five long coarse teeth. Hind tibia with two strong, apical spines. 34. Sterna with rather long hairs, many of them with a few branches.

Thrincohalictus resembles *Halictus s. str.* in its general appearance, apical tergal bands, yellow markings on the clypeus and legs of males, short and rather simple gonostylus of the male, etc. It differs from *Halictus* in the elongate head, including the malar area, labrum, and proboscis, the

FIG. 77. *Thrincohalictus prognathus*. Face of male, face and wing of female. Scale line = 1.0 mm.

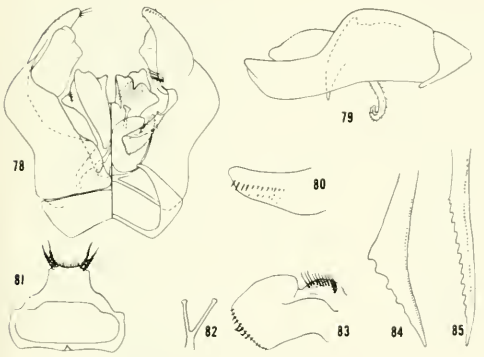
short fourth sternum of the male armed with coarse bristles apically, and the large retrorse lobe of the male genitalia. In these features it resembles *Thrinchostoma,* from which it differs, however, in so many features that there appears to be no close relationship. The fourth sternum of the male and the reduced angles at the ends of the clypeal truncation of the female suggest a relationship to the *Thrinchostoma-Patellapis-Zonalictus-Pachyhalictus* group rather than to *Halictus* and *Lasioglossum.* Among these genera, the similarity appears closest to *Patellapis,* some species of which have apical tergal hair bands and an elongate head and mouthparts (*P. braunsella*), but the simple gonostyli, shorter sternum VIII, almost complete lack of the pygidial plate of the male, yellow markings of the male, as well as the manner of head elongation (with long malar area) and other features distinguish *Thrincohalictus* from *Patellapis.*

Thrincohalictus contains only one known species, *T. prognathus* (Pérez, 1912), new combination, which ranges from the Armenian S.S.R. and Iran to the Aegean islands (Chios) and south to Israel. Its distinctiveness from relatives in Africa and tropical Asia and its distribution is suggestive of another monotypic genus, *Exoneuridia,* the only north temperate allodapine bee.

Genus *Thrinchostoma* Saussure

Figures 2, 78-87

1. Nonmetallic black or part of metasoma and legs, or even whole body, yellowish red; large and rather slender, 8-16 mm long. 2. Punctation of the usual sort, rather fine and often dense. 3. *Clypeus strongly produced downward and strongly protuberant forward,* 0.94 to 2.5 times as broad as long, with shining ground between punctures, upper part flat in profile. 4. Line between the lower ends of the eyes crossing clypeus above middle, much above the middle except in *T. afasciatum,* or even entirely above clypeus. 5. *Malar area conspicuous,* as long as eye and nearly four times as long as basal mandibular width to less than one third as long as basal mandibular width. 6. Paraocular area extending down as a strong lobe into clypeus. 7. Mouthparts long and slender, glossa linear and much exceeding the short galea and palpi. 8. Pronotum with horizontal dorsal



FIGS. 78-85. Structures of *Thrinchostoma.* 78, 79. Dorsal, ventral and lateral views of male genitalia of *T.* (*Eothrincostoma*) *producta.* 80. Posterior lateral view of gonostylus of same. 81. Eighth sternum of same. 82. Inferior basal process of penis valve of *T.* (*Thrinchostoma*) *sjostedi.* 83. Posterior lateral view of male gonostylus of same. 84, 85. Inner hind tibial spur of female of *T.* (*T.*) *afasciatum* and *T.* (*E.*) *producta.*

surface one half to twice as long medially as flagellar width, densely tomentose, margined anteriorly by an angle or carina, almost on same level as and not overhung by anterior part of scutum. 9. Dorsolateral angle of pronotum obtuse or right angular, a rounded ridge but no carina extending downward from it. 10. *Anterior extremity of scutum gently convex,* without subvertical zone separated by angle from most of scutal surface. 11. Pre-episternal groove less conspicuous than in most Halictinae, short and shallow below scrobal groove. Metanotum incompletely tomentose. 12. Dorsal surface of propodeum much longer than metanotum, sometimes as long as scutellum. Dorsal, bare, triangular area of propodeum finely to coarsely striate to granular, rather small except in *T. afasciatum,* usually not extending laterally as far as transmetanotal suture and pit. Area behind triangular area and lateral and posterior propodeal surfaces with short hairs in addition to scattered long ones. Posterior surface of propodeum margined by carinae only below, rather sharply rounding onto dorsal surface. 13. Apical wing veins strong. *Recurrent veins usually both entering third submarginal cell,* but first recurrent sometimes interstitial or entering distal extremity of second submarginal cell. 14. Third submarginal cell of moderate length, third transverse cubital vein straight or in *Eothrincostoma,* sinuate. 15. Stigma rather small and slender. Marginal cell rather slender, free part less than twice as long as part subtended by submarginal cells, apex minutely truncate and appendiculate. 16. First metasomal tergum about as long as broad. 17. Basal tergal bands of tomentum as well as apical fasciae of plumose hairs absent. 18. Apical margins of terga I-IV to III-IV of females and I-V to III-V of males usually broadly depressed, impunctate, with *golden to whitish simple hairs directed laterally,* forming bands that are conspicuous in certain lights, except in *T. afasciatum.*

Male: 19. Commonly apex of clypeus, labrum, tarsi, sometimes tibiae and rest of clypeus, yellowish white. 20. Labrum with strong apical process margined with bristles, without keel. Mandible simple. 21. Flagellum elongate, segments longer than broad, first shorter than the others, apical segment often flattened and curved (not expanded), sometimes pointed. (A few species of *Thrinchostoma s. str.* have male antennae only 12-segmented, but they are otherwise typical members of their species group, see Blüthgen, 1930.) 22. Basitibial plate not or scarcely recognizable. *Hind tibia with pallid inner apical enlargement which carries the tibial spurs far from basitarsus and from one another.* 23. First two hind tarsal segments fused, a weak constriction indicating point of union. 24. Metasoma rather elongate, parallel sided or widest at third or fourth segment. 25. Pygidial plate represented by a smooth, shining area, *not delimited by a carina either posteriorly or laterally,* this smooth area curving over onto reflexed ventral part of tergum VII. 26. Sternum IV broadly emarginate posteriorly, median part much shortened and hidden or nearly so by III (except in *T. orchidarum*), but lateral parts extending far posteriorly. Sternum V weakly to strongly emarginate apically, with basal transverse thickening or raised area, sometimes spiculate or with large pegs or hooked bristles, this thickening often hidden under IV and absent in *T. orchidarum;* sternum VI often with basal elevation frequently exposed by emargination in V. 27. Sternum VII a slender, transverse bar with median apical pointed process. Sternum VIII large with broad, truncate apical process provided with hairs. 28. Genitalia with general form of a typical halictid, the gonobase somewhat narrow, the gonocoxites broad. Gonostylus large and elaborate, half as long to as long as gonocoxite, with ventral basal membranous lobe reflexed mesally or downward and dorsal mesal membranous flap or area. Penis valve

FIG. 86. Top row: *Thrinchostoma* (*Eothrincostoma*) *producta,* face of male, face and wing of female. Middle row: *Thrinchostoma* (*Thrinchostoma*) *sjostedi,* face of male, face and wing of female. Bottom row: *T.* (*T.*) *afasciatum,* face and wing of holotype female. Scale line = 1.0 mm.

with inferior basal process very slender, capitate or bifid. (Genitalia and hidden sterna examined only for *Thrinchostoma s. str.* and *Eothrincostoma.*)

Female: 29. Scape reaching beyond anterior ocellus; first flagellar segment longer than wide. 30. Labrum with moderate to broad tapering apical process with keel; *body of labrum less than twice as wide as long.* 31. Outer surface of hind tibia with hairs largely simple, usually some branched hairs along upper margin and large curved branched hairs along basal half of lower margin. (Hairs most branched in *Eothrincostoma,* intermediate in *Thrinchostoma s. str.,* nearly all simple in *Diagonozus*). 32. Basitibial plate small, triangular, elevated above surrounding area, but without marginal ridge, surface smooth, with scattered pits, or with large grooves. 33. Inner

hind tibial spur rather finely serrate or with broad median tooth beyond which it is coarsely toothed. Hind tibia with one long, slender, tibial spine. 34. Sterna without distinctive scopa.

The Asiatic species of *Thrinchostoma* were reviewed by Blüthgen (1926), the African species, by the same author (1930). Various species have been described since those dates, however.

KEY TO THE SUBGENERA OF *Thrinchostoma*

1. Forewing without an area of dense hairs along second transverse cubital vein, this vein simple and straight; first transverse cubital arising far from base of vein r and margin of stigma; sternum IV of male with a series of enormous simple setae arising from margin both medially under sternum III and laterally, under the lateral extremity of tergum IV, where the setae are largest ..... *Eothrincostoma*

.... Forewing with an area of dense hairs near median part of second transverse cubital vein, in males these hairs forming conspicuous dark spot; second transverse cubital vein usually angulate or thickened medially, sometimes incomplete (not reaching marginal cell); first transverse cubital arising very near margin of stigma; sternum IV of male without coarse, specialized setae 2

2. Head extraordinarily produced below eyes, malar area nearly as long as or longer than eye, several times as long as basal width of mandible ....*Diagonozus*

.... Head only moderately produced below eyes, malar area much shorter than eye, three times as long as basal width of mandible or less .... *Thrinchostoma s. str.*

Subgenus *Eothrincostoma* Blüthgen

Figures 78-81, 85, 86

Eothrincostoma Blüthgen, 1930, Mitt. Zool. Mus. Berlin, 15:501.

Type species: *Halictus torridus* Smith, 1879, designation of Sandhouse, 1943, Proc. U. S. Nat. Mus., 92:548.

Clypeus moderately produced below lower ends of eyes; malar area about as long as wide. Fore wing without area of dense hairs on second transverse cubital vein. First transverse cubital arising well away from margin of stigma so that vein r is nearly as long as anterior margin of second submarginal cell; third submarginal cell strongly narrowed anteriorly (i.e., toward costal margin of wing), anterior margin less than half as long as posterior margin; second transverse cubital vein nearly straight, not angulate or thickened, complete. Inner hind tibial spur of female with inner margin rather finely and uniformly serrate, each tooth occupying about as much space as three of the very fine teeth on other margin. Fourth metasomal sternum of male with apical row of enormous bristles, bent near apices, smaller medially where they arise under the margin of sternum III, larger laterally where the bases are under the lateral margins of tergum IV, and smaller again near apices of lateral processes, also under lateral margins of tergum IV. Sternum V with a pair of similar large discal bristles. Sternum VI with preapical thickening which is densely hairy posteriorly, the hairy area narrowly divided by longitudinal hairless band.

This subgenus is more like ordinary halictids than the other subgenera in its wing venation and lack of a hair spot on the wings. Moreover, its male antennae and other features do not exhibit the special features found in many species of *Thrinchostoma* proper. *Eothrincostoma* is presumably more primitive than and probably ancestral to *Thrinchostoma s. str.*

Eothrincostoma ranges widely over tropical Africa, southward to Natal. The following is a list of species:

malelanum Cockerell, 1937
manyemae Cockerell, 1932
patricium (Strand, 1910)
silvaticum Blüthgen, 1930
torridum (Smith, 1879)
wellmani Cockerell, 1908

Subgenus *Thrinchostoma* Saussure s. str.

Figures 2, 82-84, 86

Thrinchostoma Saussure, 1890, *in* A. Grandidier, Histoire Physique, Naturelle et Politique de Madagascar, 20(1):52.

Type species: *Thrinchostoma renitantely* Saussure, 1890 (monobasic).

Trichostoma Dalla Torre, 1896, Catalogus Hymenopterorum, 10:381 (unnecessary emendation of *Thrinchostoma*); Friese, 1909, Die Bienen Afri-

kas, p. 150, *in* L. Schultze, Zoologische und Anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Südafrika, vol. 2, part 2.

Thrincostoma Dalla Torre, 1896, Catalogus Hymenopterorum, 10:641 (unnecessary emendation of *Thrinchostoma*).

Trinchostoma Sladen, 1915, Canad. Ent., 44:214 (unnecessary emendation of *Thrinchostoma*).

Rostratilapis Friese, 1914, Tijd. Ent., 57:26.

Type species: *Halictus* (*Rostratilapis*) *macrognathus* Friese, 1914, designation of Sandhouse, 1943, Proc. U. S. Nat. Mus., 92:597.

Nesothrincostoma Blüthgen, 1933, Mitt. Zool. Mus. Berlin, 18:364.

Type species: *Thrinchostoma serricorne* Blüthgen, 1933 (monobasic).

Clypeus but little (*T. afasciatum*) to moderately produced below lower ends of eyes; malar area one third to three times as long as wide. Fore wing with area of dense hairs near middle of second transverse cubital vein, these hairs forming conspicuous dark spot (minute in *T. serricorne*) in males. First transverse cubital vein arising very near to stigma so that vein r is short (about twice as long as vein width in *T. serricorne*) or virtually absent; third submarginal cell only moderately narrowed anteriorly (i.e., toward costal margin of wing), anterior margin over half as long as posterior margin; second transverse cubital usually at least slightly angulate medially in area of dense hairs, sometimes absent anterior to that point, usually also thickened medially. Inner margin of inner hind tibial spur markedly widened near middle by broad obtuse tooth, beyond which margin is coarsely toothed (Fig. 84 for *afasciatum*) to almost smooth and edentate. Sternum IV of male often with long setae on posterior lateral prolongations, but without row of very coarse setae, but such setae often present on basal thickening of sternum V. Sternum VI usually unmodified.

T. orchidarum should be restudied and its genitalia examined for possible distinctive features (type in British Museum). In this species, which is more hairy than others, the sterna II to IV are similar in form; IV is broadly exposed, but somewhat shorter than the preceding ones. Sterna II to IV each bears a preapical fringe of long hairs, broken medially. Sternum V has no basal thickening, and has a dense continuous preapical fringe. Thus, the sterna are less modified than usual in the genus.

This subgenus is widespread in tropical Africa southward to Natal, in Madagascar and in tropical Asia from south India and Assam eastward to Vietnam, Kalimantan and Java.

The following is a list of included species:

aciculatum Blüthgen, 1928
afasciatum new species
affine Blüthgen, 1928
albitarse Blüthgen, 1933
amanicum (Strand, 1910)
assamense Sladen, 1915
atrum Benoist, 1962
bequaerti Blüthgen, 1930 and form *ochropus* Blüthgen, 1930
bibundicum (Strand, 1910) and form *tessmanni* Strand, 1912
bryanti Meade-Waldo, 1914
castaneum Benoist, 1945
conjungens Blüthgen, 1933
emini Blüthgen, 1930
flaviscapus Blüthgen, 1926
fulvipes Blüthgen, 1933
fulvum Benoist, 1945
insulare Benoist, 1962
joffrei Benoist, 1962
kandti Blüthgen, 1930
lemuriae Cockerell, 1910
lualiense Cockerell, 1939
macrognathum Friese, 1914 and form *brunneum* Blüthgen, 1926
michaelis Cockerell, 1932
millari Cockerell, 1916
mwangai Blüthgen, 1930
nachtigali Blüthgen, 1930
obscurum Blüthgen, 1933
orchidarum Cockerell, 1908
othonnae Cockerell, 1908
perineti Benoist, 1962
petersi Blüthgen, 1930
productum (Smith, 1853)
renitantely Saussure, 1891
rugulosum Benoist, 1962
sakalavum Blüthgen, 1930
serricorne Blüthgen, 1933
sjostedti (Friese, 1908) and form *rufescens* (Friese, 1908)
sladeni Cockerell, 1913

telekii Blüthgen, 1930
tokinense Blüthgen, 1926
ugandae Blüthgen, 1930
umtaliense Cockerell, 1936
undulatum Cockerell, 1936
vachali Blüthgen, 1930
wissmanni Blüthgen, 1930

Subgenus *Diagonozus* Enderlein

Figure 87

Diagonozus Enderlein, 1903, Berlin Ent. Zeitschr., 48:35. Type species: *Diagonozus bicometes* Enderlein (monobasic).

Lower part of head enormously produced so that head is about as long as thorax; clypeus entirely below lower ends of eyes; malar area about four times as long as basal width of mandible, nearly as long as eye to longer than eye. Fore wing as described for *Thrinchostoma s. str.*, but third submarginal cell with anterior margin about half as long as posterior margin, second transverse cubital vein unusually strongly angulate and thickened. Inner hind tibial spur as described for *Thrinchostoma s. str.*

FIG. 87. *Thrinchostoma* (*Diagonozus*) *lettow-vorbecki*. Face and side view of head of female. Scale line = 1.0 mm.

Males have not been seen by me although described by Blüthgen (1930).

Another distinctive character of the subgenus is the more elongate pronotum, the dorsal surface of the elevated portion on the midline being considerably longer than the diameter of an ocellus. In other subgenera this length is little if any longer than an ocellar diameter. The proboscis of *Diagonozus* is also extremely long, although relative to the very long head it is little or any longer than that of *Thrinchostoma s. str. Diagonozus* appears to be a derivative of *Thrinchostoma s. str.*, recognizable primarily by the elongate head and proboscis.

Diagonozus is known from tropical west Africa. Included species are as follows:

bicometes (Enderlein, 1903)
ghesquierei Cockerell, 1932
guineense Blüthgen, 1930
lettow-vorbecki Blüthgen, 1930

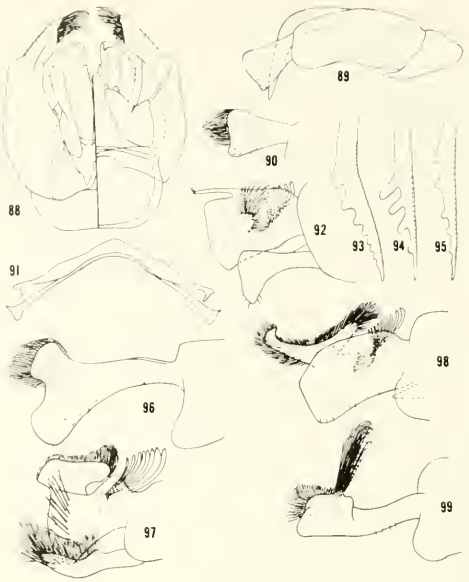
Genus *Halictus* Latreille

Figures 3-5, 88-101

1. Nonmetallic black or with body dull greenish or bluish, metasoma sometimes partly or wholly red; body length 3.5 to 17 mm. 2. Punctation of the usual sort, often fine and dense, but surfaces sometimes shining with widely separated punctures. 3. Clypeus of females and some males not much produced or protuberant, but in some males strongly produced downward and protuberant forward, nearly four times as wide as long (e.g., female of *H. squamosus*) to less than twice as wide as long (males of various species), *angle at end of truncation strongly produced in female, usually acute as seen from front, absent in male;* surface usually with shining interspaces among punctures, usually distinctly more convex near apex than near base. 4. Line between lower ends of eyes usually crossing clypeus near or above middle, but variable, in *H. squamosus* near lower margin of clypeus. 5. Malar area linear or in some males nearly half as long as wide, widest near anterior margin. 6. Paraocular area not extending down as lobe into clypeus or at most forming an obtuse or right angular lobe. 7. Distal parts of proboscis short, glossa not much longer than labial palpi or postpalpal part of galea. 8. Pronotum with subhorizontal dorsal surface medially about one third as wide as flagellar diameter, often minutely tomentose, margined anteriorly only by declivity of pronotal surface and sometimes sloping anteriorly so that it merges with the declivous surface. 9. Dorsolateral angle of pronotum usually obtuse, sometimes right angular, not lamellate or strongly carinate, a ridge extending toward posterior lobe of pronotum, but usually not extending across lobe, another ridge (rounded in most *Vestitohalictus*) extending down from dorsolateral angle. 10. Anterior extremity of scutum strongly convex in profile, the largely impunctate vertical anterior zone rising well above pronotum, usually rounding onto dorsal surface, but rarely with a sharp angle between anterior and dorsal surfaces,

anterior zone strongly bilobed in *H. squamosus* because of deeply impressed longitudinal median line of front part of scutum. 11. Pre-episternal groove often short and shallow below scrobal groove. Metanotum tomentose or not. 12. Dorsal surface of propodeum longer than metanotum, shorter than to as long as scutellum, striate to granular. Triangular area sometimes defined by end of striate or granular zone, variable in extent. Lateral and posterior surfaces of propodeum without conspicuous short hairs in addition to long ones, not areolate. Posterior surface of propodeum margined by carinae, if at all, only below, or rarely these carinae reaching upper end of posterior surface (as in *H. sexcinctellus*). 13. Apical wing veins strong. Recurrent veins entering second and third submarginal cells or rarely first recurrent nearly interstitial with second transverse cubital. 14. Third submarginal cell somewhat elongate, third transverse cubital strongly arcuate posteriorly, straight or nearly so anteriorly, the whole vein often sinuate. 15. Marginal cell rather slender to robust, free part equal to or longer than part subtended by submarginal cells, apex narrowly truncate to pointed on wing margin. 16. First metasomal tergum broader than long or in some males longer than broad. 17. Terga with or without basal areas or bands of tomentum. 18. Terga *with apical bands of pale plumose hair* (sometimes only laterally), or rarely entire surface uniformly covered with such hair. Apical margins of terga broadly depressed, with punctation somewhat finer than on more anterior parts of terga, but punctation continuous nearly to posterior borders, at least on more anterior terga, hairs not or not strongly directed laterally, posterior margins of terga dark to transparent. Disc of tergum II sometimes with oblique hairs.

Male: 19. Clypeus, labrum, and legs usually with yellow areas, tegula sometimes with yellow. 20. Labrum over three times as wide as long, rarely less than twice as wide as long, fringed with bristles, without apical process. Mandible simple. 21. Flagellum elongate, middle segments well over 1.5 and often over 2.0 times as long as wide. 22. Basitibial plate absent or sometimes vaguely recognizable as a flattened area of the usual shape, but in no case defined by a carina. 23. First two, hind, tarsal segments apparently articulated, but base of second broader than base of third. 24. Metasoma rather slender, usually parallel sided, segments I to IV almost equally broad although II and III slightly wider than others. 25. Pygidial plate defined only at apex by a carina, the carina not curving forward and defining the plate laterally, smooth area in front of apical carina sometimes small, broader than long, but often extending far toward base of tergum forming a longitudinal shiny band, sometimes elevated to form a shining ridge, in *H. maculatus* narrowed to a longitudinal carina. 26. Sterna IV and V truncate (i.e., unmodified) to broadly emarginate, without coarse bristles. 27. Sterna VII and VIII each with median apical projection, sometimes as in *H. maculatus* blunt and short, that of VIII almost absent in



FIGS. 88-99. Structures of *Halictus*. 88, 89. Dorsal, ventral and lateral views of male genitalia of *Halictus* (*Halictus*) *ligatus*. 90. Posterior lateral view of gonostylus of same. 91. Seventh and eighth sterna of same. 92. Posterior lateral view of male gonostylus, *H.* (*Seladonia*) *confusus*. 93-95. Inner hind tibial spurs of females of *H.* (*H.*) *ligatus, latisignatus*, and *maculatus*. 96-99. Posterior lateral views of male gonostyli of *H.* (*H.*) *scabiosae, quadricinctus, rubicundus*, and *patellatus*.

H. parallelus and even emarginate in *H. farinosus*, the projections usually hairless, but either or both may bear hairs. 28. Genitalia rather broad with somewhat narrow base. Gonostylus rather simple with hairy apical or subapical dorsal lobe or elaborate with one or two clumps of bristles on inner surface, some species (subgenus *Seladonia* and *H. quadricinctus*) with a "second stylus" arising ventrolateral to major one, this being the homologue of the retrorse lobe of many halictids but directed apically rather than basally; therefore *gonostylus without retrorse ventral basal lobe*. Penis valve moderately slender, inferior basal process rather slender, rounded apically, inconspicuous.

Female: 29. Scape usually reaching posterior ocelli or even beyond, rarely only attaining anterior ocellus or in a few species (*H. desertorum, placidulus*) not reaching anterior ocellus. Second flagellar segment broader than long to at least as long as broad, first and middle flagellar segments broader than long to much longer than broad. 30. Labrum with tapering apical process with keel; body of labrum usually more than twice as broad as long, rarely less than twice as broad as long, bigibbous, the two gibbosities sometimes merged. 31. Hind tibia and its scopa of the usual form. 32. Basitibial plate of moderate size, angular to rounded apically, margin elevated or absent on anterior side in *Vestitohalictus*, surface dull,

Table 1. Major Differences between *Halictus* and *Lasioglossum s.l.*

Feature	*Halictus*	*Lasioglossum*
distal wing veins	strong	weak
apical tergal hair bands	of densely plumose hairs	absent or rarely of weakly plumose hairs
inferior basal process of penis valve	inconspicuous, slender rounded at apex	broad, truncate or obliquely truncate
inferior basal retrorse lobe of male gonostylus	absent or if present, directed apically, not retrorse	commonly present, membranous, minutely hairy

with some hairs. 33. Inner hind tibial spur coarsely serrate to pectinate. Hind tibia with one or two apical spines. 34. Sternal hairs plumose, of moderate length.

Unlike the other genera described in this paper, *Halictus* is primarily developed in the palearctic region, where it contains many species. One subgenus (*Seladonia*) is abundant throughout Africa and a very few species reach southern India. In the Western Hemisphere only about ten species occur in North and Central America and only three reach South America although one *Seladonia* is found as far south as Brazil.

Halictus is closely related to the major group of halictines in which the distal wing veins are weakened, the genus *Lasioglossum s.l. Lasioglossum* is not treated in this paper, but it seems important to indicate some of the main features by which *Halictus* and *Lasioglossum* differ, since some authors still prefer to unite these genera. Distinctive features are indicated in Table 1.

Key to the Subgenera of *Halictus*

1. Basitibial plate of female slender and not or feebly defined on anterior margin; hairless triangular area of propodeum small, not reaching posterior margin of dorsal surface of propodeum even medially. (Pubescence unusually dense and white; integument black or greenish.) ..... *Vestitohalictus*

.... Basitibial plate of female of the usual shape and defined by a ridge or carina anteriorly as well as posteriorly; hairless triangular area of propodeum larger, nearly always reaching posterior declivity medially 2

2. Integument nonmetallic, black; gonostylus of male single (double in *H. quadricinctus* and allies) ..... *Halictus*

.... Integument, at least of head and thorax, metallic greenish or bluish; gonostylus of male double; i.e., two apparently separate gonostyli on apex of gonocoxite, the outer inferior one equivalent to the retrorse lobe of some halictids, but directed apically and in *H. hesperus* and *lutescens* much reduced ..... *Seladonia*

Subgenus *Seladonia* Robertson

Figures 6, 92

Seladonia Robertson, 1918, Ent. News, 29:91.

Type species: *Apis seladonia* Fabricius, 1794, by original designation.

Pachyceble Moure, 1940, Arq. Zool. Est. São Paulo, 2:54.

Type species: *Pachyceble lanei* Moure, 1940, by original designation and monotypy.

Length 4.5 to 10 mm. Integument of body dull greenish, sometimes bluish or brassy, that of metasoma sometimes nonmetallic black or brownish. Pubescence not especially dense or widespread although occasionally as in *H. niveocinctulus* tending to spread between basal and apical tergal bands and thus suggestive of *Vestitohalictus*. Ridge extending down from lateral angle of pronotum sharply angulate or carinate. Apex of marginal cell pointed. Basitibial plate of female defined by a ridge both anteriorly and posteriorly; inner hind tibial spur of female pectinate

with long or short teeth. Triangular area of propodeum ample in size, reaching posterior declivity medially, not margined by densely punctate area. Male gonostylus double (outer, inferior "stylus" reduced, but present in *H. lutescens* and *H. hesperus* of the American tropics); major gonostylus usually with a clump of coarse setae on inner surface.

This is the most widespread subgenus of *Halictus*, being found in the Holarctic region, south in the Western Hemisphere to Brazil, in Africa to the Cape of Good Hope, and into India and Southeast Asia. It is morphologically compact and unified.

The following is a list of species names placed in *Seladonia:*

abuensis Cameron, 1908
adolphi-frederici Strand, 1911
aeneobrunneus Pérez, 1895
aerarius Smith, 1873
atroviridis Cameron, 1906
austrovagans Cockerell, 1932
banalianus Strand, 1911
benguellensis Cockerell, 1908
caelestis Ebmer, 1976
candescens Cockerell, 1945
capensis Friese, 1909
centrosus Vachal, 1910
cephalicus Morawitz, 1873, and form *neuter* Blüthgen, 1923
chloropinus Cockerell, 1946
confusus Smith, 1853 and forms *arapahonum* Cockerell, 1906, *alpinus* Alfken, 1907, and *perkinsi* Blüthgen, 1925
daturae Cockerell, 1929
diductus Cockerell, 1932
dissensis Cockerell, 1945
**dissidens* Pérez, 1903
duplocinctulus Cockerell, 1940
eruditus Cockerell, 1924
expertus Cockerell, 1916
**exquisitus* Warncke, 1975
ferripennis Cockerell, 1929
**gaschunicus* Blüthgen, 1935
**gavarnicus* Pérez, 1903
gemmeus Dours, 1872
harmonius Sandhouse, 1941
hesperus Smith, 1862
hotoni Vachal, 1903
jucundiformis Cockerell, 1940
jucundus Smith, 1853
kessleri Bramson, 1879 and form *nebulosus* Warncke, 1975
komensis Cockerell, 1939
lanei (Moure, 1940)
laosina Cockerell, 1929
laticinctulus Cockerell, 1946
leucaheneus Ebmer, 1972 and form *arenosus* Ebmer, 1976
lucidipennis Smith, 1853
lutescens Friese, 1921
medanicus Cockerell, 1945
medaniellus Cockerell, 1945
**meridionalis* Morawitz, 1873
mogrenensis Cockerell, 1945
**mondaensis* Blüthgen, 1923
**mongolicus* Morawitz, 1880
**morinellus* Warncke, 1975
**mugodjaricus* Blüthgen, 1933
nikkoensis Cockerell, 1911
niloticus Smith, 1879
niveocinctulus Cockerell, 1940
**occipitalis* Ebmer, 1972
pervirens Cockerell, 1940
**petraeus* Blüthgen, 1933
**pjalmensis* Strand, 1909
**pontificus* Cockerell, 1940
propinquus Smith, 1853
pruinescens Cockerell, 1937
**secundus* Dalla Torre, 1896
seladonius (Fabricius, 1794)
seminiger Cockerell, 1937
semitectus Morawitz, 1873
silvaticus Blüthgen, 1926
smaragdulus Vachal, 1895
speculiferus Cockerell, 1929
subauratoides Blüthgen, 1926
subauratus (Rossi, 1792) and its forms *corsa* Blüthgen, 1933, and *syrius* Blüthgen, 1933
subincertus Cockerell, 1940
**subpetraeus* Blüthgen, 1933
sudanicus Cockerell, 1945

tataricus Blüthgen, 1933
tibetanus Blüthgen, 1926
tokarensis Cockerell, 1945
tokariellus Cockerell, 1945
**transbaikalensis* Blüthgen, 1933
trichiurus Cockerell, 1940
tripartitus Cockerell, 1895
tumulorum (Linnaeus, 1758)
**umbrosus* Cockerell, 1929
vansoni Cockerell, 1935
varentzowi Morawitz, 1895
varipes Morawitz, 1876
vernalis Smith, 1879
**verticalis* Blüthgen, 1931
vicinus Vachal, 1895
virgatellus Cockerell, 1901
viridibasis Cockerell, 1946
**wollmanni* Blüthgen, 1933

Subgenus *Vestitohalictus* Blüthgen

Figure 100

Vestitohalictus Blüthgen, 1961, Beitr. Naturk. Forsch. SW-Deutschl., 19:287.

Type species: *Halictus vestitus* Lepeletier, 1841, by original designation. (According to Ebmer, 1976b, this was a misidentification; Blüthgen actually had *H. pulvereus* Morawtiz. From the practical viewpoint this is of no importance, since *pulvereus* and *vestitus* are similar species of the same subgenus. The type should stand as *H. vestitus*.)

Length 3.5 to 8 mm. Integument of body dull greenish to entirely non-metallic and black, often with metasoma partly or wholly red. Pubescence dense, white or yellowish, commonly covering entirely metasomal surface, although denser on posterior margins than elsewhere. *Ridge extending down from lateral angle of pronotum rounded.* Apex of marginal cell pointed on wing margin or apex separated by a vein width or more from margin. *Basitibial plate of female undefined anteriorly, or if defined, plate narrow* and pointed below rather than broad as in other subgenera; inner hind tibial spur of female pectinate with long or short teeth. *Triangular area of propodeum small, short,* not reaching posterior declivity, usually margined posteriorly and laterally by densely punctate hairy area. Male gonostylus double as in *Seladonia* or the outer "stylus" absent.

This subgenus is found in the drier parts of the Palearctic region, from the Canary Islands and the Mediterranean basin to western China. It includes minute as well as moderate sized species, some almost wholly white because of dense pubescence, many of them with the metasomal integument partly or wholly red.

Fig. 100. *Halictus* (*Vestitohalictus*) *nasica,* face and wing of female. Scale line = 1.0 mm.

There is much diversity in the subgenus as here delimited. The type species and its close relatives (including forms with non-metallic as well as with greenish integument) have a median apical tuft or longitudinal band of dense hair on the fourth sternum of the male, but this is absent in other species. The labrum of the female in some species is quite ordinary, but in others the body of the labrum is much longer than usual (e.g., *H. desertorum,* in which it is two thirds as long as wide). The labral process is broad and very long, about twice as long as the body of the labrum in the female of *H. nasica.* In males, also, the labrum is sometimes longer than in other *Halictus,* only somewhat over twice as wide as long as in *H. desertorum.* Variation in the male gonostylus and in the basitibial plate of the female is indicated in the subgeneric description above. The most conspicuously strange feature of any female *Halictus* is the clypeus of the minute *H. nasica* which bears a long, downward projecting median process (Fig. 100).

A. W. Ebmer (in litt., 1977) questions the placement of *H. semiticus* and *H. pla-*

cidulus in the following list, and says that their male genitalia are similar to those of *Seladonia*. It may be that the problem arises in part from misassociation of sexes of *H. placidulus*, for Ebmer indicates that the female holotype has a small propodeal triangle as in *Vestitohalictus* while the male has characters suggesting a relationship with *H. (Seladonia) varentzowi*. It well may be that some species intergrade with *Seladonia*. In general, however, the two subgenera seem quite distinct.

The following is a list of species that fall in the subgenus *Vestitohalictus*.

**aenescens* (Radoszkowski, 1893)
**balearicus* Pérez, 1903
**bulbiceps* Blüthgen, 1929
**concinnus* Brullé, 1840
cupidus Vachal, 1902
cypricus Blüthgen, 1937
desertorum Morawitz, 1876
**fuscicollis* Morawitz, 1876 and form *transcaspica* Blüthgen, 1923
**indefinitus* Blüthgen, 1923
**inpilosus* Ebmer, 1975
**kuschkensis* Ebmer, 1975
**microcardia* Pérez, 1895
morawitzi Vachal, 1902 and form *theseus* Ebmer, 1975
mordacellus Blüthgen, 1929
**mordax* Blüthgen, 1923
mucidus Blüthgen, 1923
mucoreus (Eversmann, 1852)
nasica Morawitz, 1876
**ochropus* Blüthgen, 1923
persephone Ebmer, 1976
pici Pérez, 1895
placidulus Blüthgen, 1923
pollinosus Sichel, 1860 and its forms *limissicus* Blüthgen, 1937 and *thevestensis* Pérez, 1903
pulvereus Morawitz, 1873, and its form *tectus* Radoszkowsky, 1876
**pseudomucoreus* Ebmer, 1975
pseudovestitus Blüthgen, 1925
radoszkovskii Vachal, 1902
**semiticus* Blüthgen, 1955
sogdianus Morawitz, 1876
**solitudinis* Ebmer, 1975
**surabadensis* Ebmer, 1975
**tuberculatus* Blüthgen, 1925
**vestitus* Lepeletier, 1841

Subgenus *Halictus* Latreille s. str.

Figures 3-5, 88-91, 93-99, 101

Halictus Latreille, 1804, Nouv. Dict. Hist. Nat., 24: 182.

Type species: *Apis quadricincta* Fabricius, 1776, by designation of Richards, 1935 (see below).

Odontalictus Robertson, 1918, Ent. News, 29:91.

Type species: *Halictus ligatus* Say, 1837, monobasic and by original designation.

Monilapis Cockerell, 1931, Ann. Mag. Nat. Hist., (10)7:529.

Type species: *Hylaeus tomentosus* Eversmann, 1852, monobasic and by original designation.

The type species for the name *Halictus* has been a subject of much discussion. The following designations and interpretations exist:

1. *Apis sexcincta* Fabricius, 1775, "ejusd." *Andrena rufipes* Fabricius, 1793, designation by Latreille, 1810, Considérations générales . . . des insectes, p. 439.
2. *Apis rubicunda* Christ, 1791, designation by Curtis, 1833, British Entomology, 10:448a.
3. *Apis quadricincta* Fabricius, 1776, designation by Richards, 1935, Trans. Royal Ent. Soc. London, 83:170.
4. *Andrena rufipes* auctorum, nec Fabricius = *Apis sexcincta* Fabricius, 1775. This is the interpretation of Latreille's designation by Warncke (1975).
5. *Andrena rufipes* Fabricius, 1793. This is the interpretation of Latreille's designation by Ebmer (1974, 1976a).

The only species included by Latreille in 1804 were *rufipes, quadricinctus,* and *flavipes*. Designation number 2 is there-

fore invalid for it clearly involves a species not originally included.

The problems center around designation number 1, of which numbers 4 and 5 are interpretations. This designation is invalidated by Opinion number 136 of the International Commission on Zoological Nomenclature (1939), which takes the position that when Latreille in his tabulation of 1810 listed two or more trivial names, there was no type designation.

Even if one ignores Opinion 136, the conclusion is the same. The abbreviation *"ejusd."* in Designation 1 is for *ejusdem* or *ejusdemmodi,* meaning "in the same way." One might assume that this means "the same species," and that Latreille was therefore synonymizing *rufipes,* an originally included name, with *sexcinctus,* which was not included by name, but has priority, at the same time that he stated the type species. The International Code of Zoological Nomenclature [Article 69, (a) (iv)] states that if an author designates a type species using a name that was not originally included, but at the same time synonymizes that name with one of the originally included species, the designation of the latter as type species is valid. Thus Latreille's act would be considered as designation of *Apis sexcinctus* as the type species. It is irrelevant that the so-called type specimen of *Andrena rufipes* is a wasp which does not agree with the original description at all well (Ebmer, 1976a). There is no need to draw the distinction that Warncke (1975) makes between *rufipes* acutorum (the bee) and *rufipes* Fabricius (the wasp), for the wasp with the label *"rufipes"* must be a result of a probably post-Fabrician error. Under the circumstances, it is also irrelevant that *rufipes* and *sexcinctus* are not now considered synonymous (Ebmer, 1974, 1976a).

In reality, Latreille (1810) did not use *"ejusd."* to indicate synonymy. He listed together species that were not at all alike, but that agreed in what he considered as generic characters. For example, for the genus *Megachile* he lists *muraria* Fab. *ejusd. lanata, argentata,* and *centuncularis.* These are extremely different looking species; he could not have been suggesting specific synonymy. The same is true for *Centris* where he lists *haemorrhoidalis ejusd. versicolor,* two differently colored and clearly nonsynonymous species. Thus for *Halictus,* he was evidently saying "the type is *sexcinctus,* and *rufipes* also belongs here." Since *sexcinctus* was not an originally included species, Latreille's "designation" is invalid.

Ebmer (1976a) has argued that since Latreille, in indicating the type species, listed two species, only one of which was originally included, that one (*rufipes*) is thereby designated as the type. This view does not appear to be justified by Article 69 of the International Code of Zoological Nomenclature. Moreover, as already indicated, in view of Opinion 136, all such considerations are irrelevant in any event.

Presumably, it was for the reasons outlined above that Richards made the only valid type designation, number 3 above, the species being *Apis quadricincta* Fabricius.

Warncke (1970, see also 1975) designated the same *Apis quadricincta* Fabricius as the type species of *Hylaeus,* a name proposed by Fabricius in 1793. This designation would have the effect of making *Hylaeus* available as a senior synonym of *Halictus.* Warncke's designation is invalid since Latreille in 1810 designated a different species, *Apis annulata* Linnaeus, as the type species of *Hylaeus.* This is a species belonging to the genus known in most parts of the world today as *Hylaeus.* Latreille's designation may have been unfortunate at the time, for *annulata* was the only species of its genus included by Fabricius under the name *Hylaeus,* compared to six species of Halictinae, and the name

Hylaeus was widely although not uniformly used at one time for the group now known as Halictini. Nonetheless, *Apis annulata* was one of the species originally included in *Hylaeus* and the designation is valid. There is no legitimacy to Warncke's argument that *Hylaeus* of Latreille is a different genus with a different type species from *Hylaeus* of Fabricius.

Length 6 to 17 mm. Integument of body nonmetallic, black or brownish, the metasoma rarely partly red. Pubescence not especially dense or widespread, metasomal terga usually without basal bands of hair but with apical bands only, in the *H. senilis* group hair dense, widespread, often white. Ridge extending down from lateral angle of propotum sharply angulate or carinate. Apex of marginal cell minutely truncate to pointed on wing margin. Basitibial plate of female defined by a ridge both anteriorly and posteriorly; inner hind tibial spur of female coarse serrate to short pectinate, or the teeth long in *H. latisignatus*. Triangular area of propodeum ample in size, reaching posterior declivity medially, not margined by densely punctate area. Male gonostylus usually not double, with or without one or two tufts of coarse setae on inner surface, gonostylus double (i.e., with the equivalent of the retrorse lobe projecting distally) only in *H. quadricinctus* and its immediate allies such as *H. brunnescens*.

The subgenus *Halictus* is abundant in the Palearctic region. It does not occur, however, in subsaharan Africa or in southeast Asia and only one species (*H. latisignatus*) reaches southern India. Only four species occur in North America. One of them, *H. rubicundus,* is Holarctic and one, *H. ligatus,* extends southward into the Neotropical region as far as Colombia and Trinidad.

The subgenus *Halictus* contains several diverse elements, probably as different from one another as they are from *Seladonia*. The latter subgenus, however, is easily recognized in both sexes by its greenish coloration while the groups included in *Halictus* proper are all non-metallic and the females are difficult to segregate into groups. Since for many species, only females are known or males have not been available for dissection, I have not been able to place numerous names as to group. If the subgenus were divided now, many species would therefore not be assignable to subgenus. For this reason, subdivision has not been formally proposed. The groups, however, are distinguishable by the characters of males listed below, and are numbered 1 to 4. These numbers in front of names in the list of species indicate the groups to which certain species belong. (Since writing the above, A. W. Ebmer of Linz, Austria, the principal specialist on Palearctic halictines, has been kind enough to examine my groupings. In general, he agrees with them and has placed nearly all the species not only in these groups, but in subdivisions thereof. I leave to him the full account of groups or subgenera and placement of the species.)

Group 1

Mandible broadened basally. First flagellar segment much broader than long; flagellum somewhat moniliform. Hypostomal area concave. Malar space present. Sternum IV with apical margin broadly concave, sternum longest at extreme sides. Gonostylus not double, somewhat expanded apically, usually with a clump of long, coarse setae on inner surface, but such setae absent in some species such as *H. simplex*.

The name *Monilapis* is available for Group 1 and could be used in a subgeneric sense except for the problem of placing species known only from females, as mentioned above. The name "tetrazonius group" has usually been used. It is a compact, Palearctic group characterized by a series of derived features. The clump of coarse setae usually arising from the inner surface of the gonostylus is probably homologous to the coarse setae on the basal extension of the preapical hairy lobe in Group 3. It is not homologous to the clump of specialized, flattened setae found in Group 3 and *Seladonia*.

Group 2

Mandible not broadened basally. First flagellar segment slightly broader than long to longer than broad; flagellum not moniliform. Hypostomal area not concave. Malar space variable. Sternum IV sim-

ple or with margin concave, longest sublaterally so that if margin is concave, the posteriormost angles are mesal to the sides of the sternum. Gonostylus not double, relatively simple, with hairy inner apical or preapical lobe, but without a clump of long coarse setae on inner surface.

The name *Odontalictus* is available for this group, which is restricted to the Palearctic region except for *H. ligatus* which is American. The genal tooth of the female of *H. ligatus,* which led Robertson to provide the name *Odontalictus,* is not a subgeneric or group character. It is also found in some unrelated Palearctic species such as *H. modernus* and *submodernus* and even in *H.* (*Seladonia*) *wollmanni. H. ligatus* is in the *scabiosae* subgroup of my Group 2.

Group 3

Agrees with Group 2 except as follows: sternum IV, if concave, longest at lateral margins as in Group 1. Gonostylus complex, with preapical, hairy lobe which often projects both basally and apically, and with clump of coarse, flattened setae on inner surface basal to the lobe; sometimes (e.g., in *H. rubicundus*) with small outer inferior "stylus," this fully developed so that the stylus appears double in *H. quadricinctus* and its allies.

The double gonostylus of *H. quadricinctus* and its allies is suggestive of that of *Seladonia,* as is the clump of specialized setae arising from the inner surface of the gonostylus, but the large, nonmetallic species of Group 3 and the small, greenish species of *Seladonia* do not superficially appear closely related.

FIG. 101. *Halictus* (*Halictus*) *farinosus,* face of male, face and wing of female. Scale line = 1.0 mm.

The name *Halictus s. str.* is available for this group, which is restricted to the Palearctic region except for three species found in North America.

Group 4

Mandible not broadened basally. First flagellar segment longer than broad, flagellum not moniliform. Hypostomal area not concave. Malar area linear. Sternum IV with apical margin concave, sternum widest laterally; V deeply emarginate, VI with large median hairy area. Gonostylus not double, with broad, scarcely hairy, thin lobe extending downward and slender apical process projecting in same direction, with clump of long coarse setae on inner surface, but this displaced basad relative to other species so that it arises basal to apex of gonocoxite.

This group contains only the Indian species *H. latisignatus,* which is distinguishable in the female by the small median elevation on the apical margin of the clypeus. The distinctive features have been well illustrated by Sakagami and Wain (1966).

The following is a list of species of the subgenus *Halictus:*

**acrocephalus* Blüthgen, 1923
**adjikenticus* Blüthgen, 1923
(3) *aegyptiacus* Friese, 1916
(1) *aegypticola* Strand, 1909
**albohispidus* Blüthgen, 1923
**albozonatus* Dours, 1872
**alfkenellus* Strand, 1909
**altaicus* Pérez, 1903
asperatus Bingham, 1898
asperulus Pérez, 1895
**atripes* Morawitz, 1894
**aureipes* Dours, 1872
**bagirensis* Blüthgen, 1936
(2)**berlandi* Blüthgen, 1936
(1)**bifidus* Warncke, 1975
**brunnescens* (Eversmann, 1852)
**bucharicus* Blüthgen, 1936
(1)**carinthiacus* Blüthgen, 1936
(2)**cedens* Blüthgen, 1931
(2) *cochleariturs* (Dours, 1872)
**consobrinus* Pérez, 1895
(2) *constantinensis* Strand, 1910
(2) *constrictus* Smith, 1853

(1)*crenicornis* Blüthgen, 1923
cyrenaicus Blüthgen, 1930,
determinandus Dalla Torre, 1896
dschulfensis Blüthgen, 1936
dunganicus Blüthgen, 1936
(1)*eurygnathopsis* Blüthgen, 1936
(1) *eurygnathus* Blüthgen, 1930
(3) *farinosus* Smith, 1853
(2)*fatsensis* Blüthgen, 1936
fimbriatus Smith, 1853
formosus Dours, 1872
(2) *frontalis* Smith, 1853
fucosus Morawitz, 1876
(2) *fulvipes* (Klug, 1817)
fumatipennis Blüthgen, 1924
funerarius Morawitz, 1876
(1)*furcatus* Blüthgen, 1925
georgicus Blüthgen, 1936
gordius Warncke, 1975
(2)*graecus* Blüthgen, 1936
(1)*grunwaldti* Ebmer, 1975
gusenleitneri Ebmer, 1975
hedini Blüthgen, 1935
holomelaenus Blüthgen, 1936
(2)*humkalensis* Blüthgen, 1936
(2)*hybridopsis* Blüthgen, 1923
intumescens Pérez, 1895
jaramielicus Blüthgen, 1923
kusdasi Ebmer, 1975
(1) *langobardicus* Blüthgen, 1944
(4) *latisignatus* Cameron, 1908
libanensis Pérez, 1911
(2) *ligatus* Say, 1837
(2)*luganicus* Blüthgen, 1936
lunatus Warncke, 1975
lussinicus Blüthgen, 1935
(2) *maculatus* Smith, 1848 and form
priesneri Ebmer, 1975
marchali Vachal, 1891
maroccanus Blüthgen, 1933
mediterranellus Strand, 1909
minor Morawitz, 1876
modernus Morawitz, 1876
(2) *nadigi* Blüthgen, 1933
nicosiae Blüthgen, 1923
ochraceovittatus Dours, 1872
palustris Morawitz, 1876
(3) *parallelus* Say, 1837
(1) *patellatus* Morawitz, 1873
pentheri Blüthgen, 1924
(1)*ponticus* Blüthgen, 1936
pseudomaculatus Blüthgen, 1925
pseudotetrazonius Strand, 1921
(1) *pyrenaeus* Pérez, 1903
(2)*quadricinctoides* Blüthgen, 1936
(3) *quadricinctus* (Fabricius, 1776)
(1)*quadripartitus* Blüthgen, 1923
(3) *rubicundus* (Christ, 1791) and forms
mongolensis Blüthgen, 1936,
laticinctus Blüthgen, 1923, and
lerouxii Lepeletier, 1841
(3) *rufipes* (Fabricius, 1793)
sajoi Blüthgen, 1923
(1)*samarensis* Blüthgen, 1936
(2) *scabiosae* (Rossi, 1790) and form
powelli Cockerell, 1931
(1)*scardicus* Blüthgen, 1936
sefidicus Blüthgen, 1936
senilis (Eversmann, 1852)
sepositus Cockerell, 1921
(2) *sexcinctus* (Fabricius, 1775)
(1)*siculus* Blüthgen, 1925
(1) *simplex* Blüthgen, 1923 (=*ibex* Warncke, 1973)
squamosus Lebedev, 1910
stachii Blüthgen, 1923
(2)*subalfkenellus* Blüthgen, 1936
submodernus Blüthgen, 1936
(2)*subsenilis* Blüthgen, 1955
takuiricus Blüthgen, 1936
(1) *tetrazonianellus* Strand, 1909
(1) *tetrazonius* Klug, 1817
tibialis Walker, 1871
tomentosus (Eversmann, 1852)
tridivisus Blüthgen, 1923
tsingtouensis Strand, 1910
turanicola Dalla Torre, 1896
(2)*turkomannus* Pérez, 1903
wagneri Blüthgen, 1937
(1) *wjernicus* Blüthgen, 1936
yarkandensis Strand, 1909

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I am especially pleased to acknowledge the help of P. Andreas W. Ebmer of Linz, Austria, with regard to the lists of species of *Halictus*. Not wishing to detract from his future publications, I have not incorporated all the information which he provided relative to groupings, synonymies, and the like, but I have incorporated many additions and corrections received from him.

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Appendix

The following are new species described so that their characters can be incorporated into the descriptions in the body of this paper, plus certain other taxonomic notes that relate to these bees.

Patellapis (*Patellapis*) *braunsella* new species

Figures 27, 29-33, 44

In its elongate head and associated features such as the long glossa and the lobe of the paraocular area cutting into the clypeus, this species differs from all other *Patellapis*. *P.* (*Lomatalictus*) *pastina* has a moderately elongate head and a somewhat long glossa, but these features are less extreme than in *P. braunsella* and must be independently evolved. *P. braunsella,* as shown by the subgeneric characters, is more closely related to *P. schultzi* and *P. minutior*. It is the size of the latter, but differs in many ways including the head shape and associated characters listed above and the more elongate and crenulate antennal flagellum.

Female: Length 8 mm; forewing length 6.5 mm. Black with dark brown on middle of mandible, under side of flagellum, and small segments of tarsi; apices of metasomal terga and sterna II to IV broadly pallid translucent. Wings clear, veins and stigma rather light brown.

Pubescence dull white, moderately abundant and long, plumose but not as heavily so as in *P. malachurina,* especially long (much longer than eye width) on genal area; longest hairs on basal half of scape nearly half as long as scape; first metasomal tergum with apical white hair band restricted to sides; base of tergum II, especially laterally, with scattered plumose white hairs (the closest approach to basal bands of tomentum found in the genus); terga II-IV with broad, well defined, dense apical hair bands. Hair of fifth tergum orange red, fading to white laterally. Tibial and tarsal hairs yellowish white, yellower on under sides of tarsi; clypeal fringe and hairs of mandible similarly yellow; penicillus orange yellow.

Head slightly longer than broad (188:162); upper and lower interorbital distances as 104:100. Clypeus slightly over twice as wide as long (98:42); line between lower ends of eyes crossing clypeus near upper margin; paraocular area extending down into clypeus as an approximately right angular lobe. Malar space linear. Inner orbits convergent below, except for upper parts, which are convergent above. Antennal sockets separated by less than diameter of a socket. Antennocular:interantennal:antennocellar:interocellar:ocellocular distances as 32:12:52:39:24. Labrum with convex body about twice as wide as long and apical pointed process shorter than body. Frontal carina ending well below level of lower margins of antennal sockets. Upper part of genal area wider than eye, area widest at upper third of eye and narrowing to almost nothing in lateral view at lower end of eye. Glossa as long as head. Scape reaching to level of upper margin of lateral ocellus; first flagellar segment about as broad as long, second broader than long, others longer than broad. Dorsolateral pronotal angles obtuse; a ridge, but no carina, extending across pronotal lobe. Dorsal surface of propodeum shorter than scutellum, separated from posterior surface by a moderately sharp angle, no distinct carina defining posterior surface laterally although several minute ridges mark the lateral limit of that surface below. Basitibial plate

rather narrowly rounded apically. Inner margin of inner hind tibial spur minutely serrate-pectinate or ciliate.

Clypeus and lower part of paraocular area shining with irregular, large, well separated punctures. Supraclypeal area minutely roughened, dull, with smaller punctures separated by over a puncture width. Frons and vertex finely and densely strigose-punctate. Genal area more coarsely and shallowly strigose. Hypostomal area nearly smooth, shining, flat. Scutum dull, minutely and closely punctured; scutellum and metanotum with much coarser punctures on a minutely roughened but shining ground. Sides of thorax and propodeum minutely reticulate or punctate with scattered large, shallow punctures. Dorsal part of propodeum minutely roughened and dull, the triangular area with a coarser pattern of fine, radiating striae laterally, medially on basal half or more of triangle such striae anastomosing to form irregular small areoleae. Metasomal terga somewhat shining, but surfaces minutely roughened, especially on more posterior terga, almost without such roughening on dorsolateral swellings in front of depressed margins of terga I and II; punctation rather fine, coarsest on above mentioned swellings, progressively finer and sparser on marginal areas, where densest punctures separated by about a puncture width. Sterna shining, but minutely roughened, hairs arising from papillae.

Male: Length 8 mm; wing length 6.5 mm. Coloration as in female but mandibular apices, under side of flagellum, and pygidial plate and adjacent areas red brown; all exposed terga and sterna except seventh tergum with broadly pallid, translucent apices.

Pubescence as described for female, but all tergal hair bands weak middorsally and even laterally not as dense as in female; terga V and VI without hair bands; base of II without tomentum. No red hair at apex of metasoma. Sterna I-IV with apical fringes of hair, sternum V with area of dense hair at each side subapically. Hair of legs, clypeal margin, and mandible nearly as white as that of body. Under sides of all trochanters and femora with particularly long white hairs; under side of hind femur except apex densely covered with such hairs, some nearly half as long as femur, mostly directed basad.

Head longer than broad (180:159) upper and lower interorbital distances as 102:82. Clypeus width: length::78:44. Line between lower ends of eyes crossing clypeus above middle. Paraocular lobe, malar space, convergence of orbits, and separation of antennal sockets as in female. Antennocular: interantennal:antennocellar:interocellar:ocellocular distances as 27:12:48:40:26. Labrum with strongly convex, shining body twice as wide as long and small obtuse angle representing apical process. Frontal carina, genal area, glossa as in female. Scape reaching middle of anterior ocellus; first flagellar segment much broader than long, others longer than broad (second over 1.5 times as long as broad), median ones crenulate. Pronotum and propodeum as in female. Basitibial plate defined by strong carina, but plate much more slender than in female and therefore with angulate apex. Sternum IV hidden by third, with row of about 22 bristles arising from premarginal thickening, lateral ones enormous and lying flat, others progressively smaller toward median ones, middle 12 bristles or thereabouts bent at about level of apical sternal margin and thereafter erect. Sternum V with apical margin broadly emarginate between sublateral lobes.

Punctation similar to that of female, but on clypeus and lower part of paraocular area denser; hypostomal area minutely roughened, not smooth and impunctate. Propodeum with minutely areolate or reticulate part of triangle extending almost to posterior margin. Tergal punctation somewhat finer than in female, punctures of first two terga separated by about a puncture width, ground shiny and smooth; more posterior terga progressively more roughened and less punctate.

Holotype male, Willowmore, Cape Province (Capland on the label), South Africa, February 1, 1905 (Dr. Brauns). Allotype female, same locality and collector, May 15, 1905. Two female paratypes, May 4 and 15, 1905 and two male paratypes, August 25, 1906 and October, 1910.

The holotype and allotype are in the Transvaal Museum, Pretoria, South Africa; a pair of paratypes is in the Snow Entomological Museum, University of Kansas, and the other pair in the British Museum (Natural History).

This species is named for the collector, the late Dr. H. Brauns, formerly of Willowmore, Cape Province.

Pachyhalictus (*Dictyohalictus*) *retigerus* (Cockerell)

Figures 62-68

Halictus retigerus Cockerell, 1940, Ann. Mag. Nat. Hist., (11)5:88.

Halictus weenenicus Cockerell, 1941, Ann. Mag. Nat. Hist., (11)8:205 (new synonym).

Halictus latifrontosus Cockerell, 1946, Entomologist, 79:43 (new synonym).

Halictus crassinervis Cockerell, 1946, Entomologist, 79:183 (new synonym).

Examination of types in the British Museum indicated that the specific names listed above are synonymous. The types of the last three were all taken at the same locality in Natal, South Africa, by the same collector. The name *crassinervis* is based on males, the others on females. The locality for the first name listed is in Rhodesia.

The following locality record extends the range to another country: one female, Vipya Plateau, 12 miles northeast of Mzimba, Malawi, 5200 feet altitude, 15 April 1967 (C. D. Michener).

Thrinchostoma (*Thrinchostoma*) *afasciatum* new species

Figures 84, 86

This species is described here because it has certain characters not otherwise found in the genus which must therefore be accounted for in the generic description. The short malar space, only one third as long as broad or perhaps less, distinguishes this species from all others except *T. sladeni* Cockerell (see Blüthgen, 1926) from Assam. The most remarkable feature, however, is the lack of the bands of pale (usually silvery), laterally directed hairs on the posterior marginal areas of the metasomal terga. Such bands characterize all other species of the genus. The incompletely described *T. bryanti* Meade-Waldo, 1914, also from Borneo, could be the male of *T. afasciatum*. It has black head and thorax, probably lacks radiating striae in the propodeal triangle, and thus seems likely to be different although the description says nothing of the apical tergal bands.

Female: Length 9.5 mm. Head brownish black; labrum, malar area, clypeus, and lower part of paraocular area testaceous, this color grading into the dark color of rest of head, supraclypeal area and hypostomal area being largely reddish brown. Mandible testaceous except for dark brown apex. Antenna brownish black except base of scape and under sides of segments 7-12 testaceous. Thorax and legs testaceous except for mesoscutum which is dusky brownish, grading to testaceous posteriorly. Wings yellowish, veins and stigma dusky brown, at extreme wing bases testaceous, also veins forming marginal cell beyond stigma and beyond third transverse cubital vein testaceous. First metasomal tergum and narrow basal bands on terga 2-4 testaceous; broad apical bands on terga 1-4 transparent so that basal testaceous bands on terga 2-4 show through; rest of metasomal dorsum brownish black; metasomal venter brown, testaceous basally.

Hair of head dull yellowish white, some of long hairs dusky in certain lights; subappressed plumose hairs almost hiding surface of lower part of paraocular area laterally; short subappressed hairs also abundant, but not obscuring surface on rest of paraocular area, frons, vertex and genal areas; long, simple, mostly subserect hairs present on most of head, unusually long, yellowish, and strongly directed forward on supraclypeal area, clypeus, mandible, hypostomal area, and lower genal area. Thoracic hair colored like that of head, short whitish hairs abundant on pleura, sides and posterior face of propodeum, and on metanotum; longer erect hairs mostly simple and dusky in certain lights dorsally, paler and often coarsely plumose laterally. Hairs of legs pale testaceous, golden on under sides of tibiae and tarsi. Metasomal hair dull yellowish white, long erect dorsal hairs dusky in certain lights; transparent marginal bands of terga 1-4 with only scattered, short, laterally directed hairs.

Head broader than thorax, clypeus 2.5 times as broad as long, not much produced downward nor protuberant anteriorly; inner orbits not strongly converging below (Fig. 86); line tangent to lower ends of eyes only a little above middle of clypeus; antennal sockets separated by more than diameter of a socket; antennocular distance about twice diameter of antennal socket; malar area about three times as wide as shortest length; mandible long, less strongly curved than in the forms with a more produced clypeus; first flagellar segment slightly longer than broad, middle segments markedly so. Interocellar distance much less than ocellocular distance. Genal area about as broad as eye seen from side. Glossa distinctly longer than length of head, apical fourth without long hairs. Inner hind tibial spur as in Figure 84. Scutellum bigibbous; dorsum of propodeum longer than scutellum. Forewing with basal vein and m-cu interstitial; submarginal cells as in Figure 81; hairs denser around the medially thickened second transverse cubital vein than elsewhere.

Clypeus and supraclypeal area shining, with coarse punctures, some of them longitudinally elongate, irregularly placed, but mostly about a puncture width apart; rest of head and thorax with minute punctures, widely separated on scutum, the center of which is shining and impunctate, scutellar gibbosities also shining and impunctate; sides of thorax mostly minutely roughened and dull; propodeal triangle large, nearly reaching declivity, with strong, regular, radiating ridges. Metasomal terga grading from the first which is shining with only scattered minute punctures to the fifth which has a dull surface and scattered small punctures; posterior transparent margins of terga I-IV impunctate, shining on tergum I, progressively duller on succeeding terga.

Holotype female: Pontianak, Borneo (Kalimantan, Indonesia) (F. Muir) in the collection of the Bishop Museum, Honolulu.

The specific name is based on *a,* without, plus *fasciatus,* banded, with reference to the lack of apical tergal bands of later-

ally directed silvery or golden hairs, characteristic of other species of the genus.

Halictus (*Seladonia*) *lutescens* Friese, 1921

Halictus ruae Cockerell, 1949, Proc. U. S. Nat. Mus., 98:446 (new synonym).

Type of *ruae* in National Museum of Natural History, Washington, D.C.

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A NEW GENUS OF CRYPTODIRAN TURTLES (TESTUDINOIDEA, CHELYDRIDAE) FROM THE UPPER CRETACEOUS HELL CREEK FORMATION OF MONTANA

By

KENNETH N. WHETSTONE

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Kenneth N. Whetstone

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ABSTRACT

Emarginachelys cretacea is described as a new genus and species of cryptodiran turtle and is placed in the Chelydridae on the basis of shared derived characters. The holotype is a nearly complete skeleton from the Hell Creek Formation (Maestrichtian) of Montana. *Emarginachelys* is the oldest known member of the superfamily Testudinoidea as defined by Gaffney (1975a). The Chelydridae are hypothesized to be a monophyletic group, sharing a cruciform plastron ligamentously attached to the carapace, a reduced entoplastron, long costiform processes on the nuchal bone, an elongate jugal, and the pectineal processes of the pubis not strongly divergent. *Emarginachelys* is hypothesized to be the most primitive genus of the Chelydridae since it does not have the derived characters shared by advanced chelydrids. Advanced chelydrids have the frontal bones separated from the orbital rim, a premaxillary "hook," constriction of the otic bridge, a closed incisura columella auris, a serrated carapacial margin, and peripheral fontanelles.

INTRODUCTION

The turtle superfamily Testudinoidea includes the majority of living turtles, both in numbers and diversity. As defined by Gaffney (1975a), the testudinoids include the pond turtles (Emydinae and Batagurinae), the tortoises (Testudininae), and the snapping turtles (Chelydridae). Previously, the oldest known definitive testudinoids were a

chelydrid, *Protochelydra zangerli*, from the Paleocene of North Dakota (Erickson, 1973), and a pond turtle, *Ptychogaster* sp., from the Paleocene of the Big Horn Basin in Wyoming (Estes, 1975). The family Chelydridae has a sparse fossil record in Tertiary deposits of North America and Europe, and only two species are extant, both restricted to the New World (Fig. 1). Gaffney (1975b) includes the Recent Asiatic genus *Platysternon* in the Chelydridae, but I do not consider this to be a parsimonious interpretation of the affinities of this genus (see discussion below).

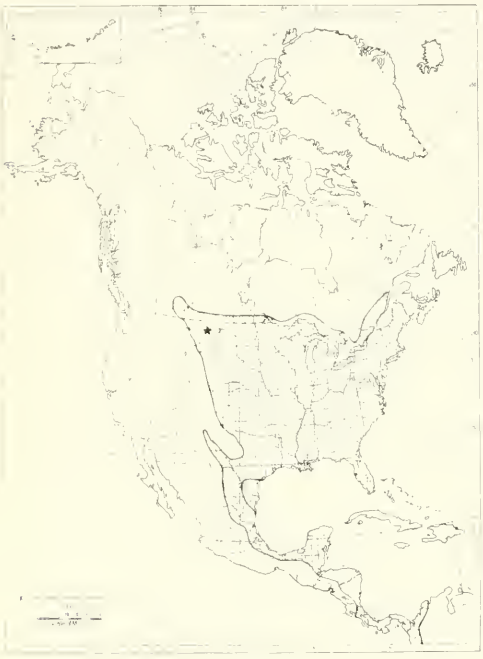

FIG. 1. Generalized distribution of recent chelydrid turtles. Star shows location from which the holotype of *Emarginachelys* was recovered.

The species described herein as *Emarginachelys cretacea* n. gen. et sp. is the oldest and most primitive species placed in the Chelydridae. A University of Kansas field party (Don and Stan Rasmussen and John Chorn) collected the holotype in 1971 from the Upper Cretaceous Hell Creek Formation in Montana. The type specimen is a nearly complete skeleton, still mainly articulated when found. Fossil turtles of this quality are extremely rare, especially in Mesozoic strata.

The turtle was preserved as a large "clast" in a medium grained sandstone which lies 5.2 m. (27 feet) below the "Z" coal of the Paleocene Ft. Union Formation (Fig. 2).

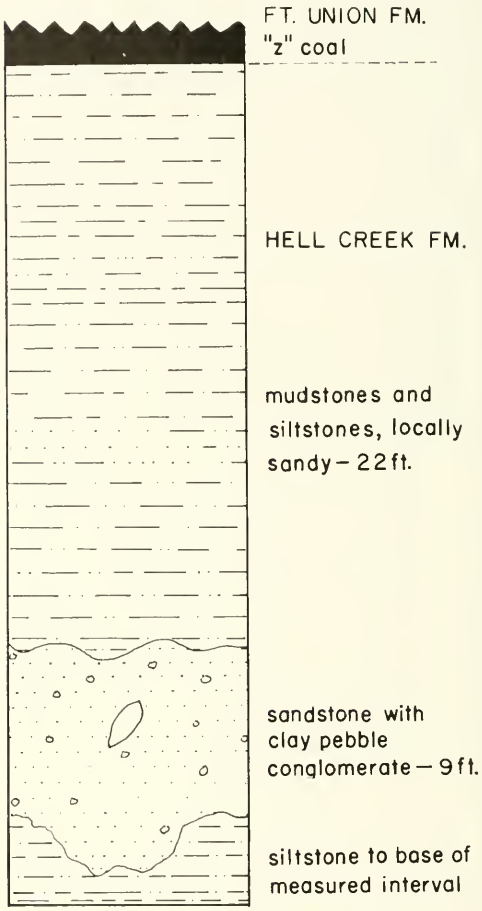

FIG. 2. Geologic section at type locality.

The Hell Creek Formation is Upper Cretaceous (Maestrichtian) in age, its uppermost strata Potassium-Argon dated at roughly 63 million years old (Gill and Cobban, 1973). The vertebrate fossils found with the specimen included scales of ganoid fishes, crocodile teeth and bones, and indeterminate dinosaur fragments. In the older literature, the Hell Creek beds were considered part of the Lance Formation, and Hell Creek specimens were often described as "from the Lance," or "from the Laramie Cretaceous" (e.g., Hay, 1908). Turtles previously known from the

Hell Creek Formation include the following baenid genera (Gaffney, 1972a): *Hayemys, Plesiobaena, Eubaena, Stygiochelys, Palatobaena,* and *Neurankylus.* Trionychids (soft shelled turtles) have been found in the Hell Creek, Lance, and Judith River Formations.

SYSTEMATIC METHODOLOGY

In this study, I name, diagnose, and describe a new taxon and formulate a hypothesis of its phylogenetic relationships.

A phylogenetic hypothesis must take the form of a three-taxon statement of the sort, "taxa A and B share a common ancestor not shared by C." Hennig (1950, 1966) shows that only shared, uniquely-derived characters (synapomorphies) can demonstrate the relative recency of common descent. A phylogenetic hypothesis is tested against alternate hypotheses and is accepted or rejected based upon the relative parsimony of the alternate hypotheses. Relative parsimony is decided by way of (cf. Nelson, 1970): (1) minimum parallel evolution, (2) anatomical and embryological similarity of presumed synapomorphous characters, (3) minimum parallel evolution of complex characters and characters buffered from requirements of similar adaptive modes of the organisms, and (4) minimum reversal of evolutionary trends. Formulation of phylogenetic hypotheses, and testing them using synapomorphous characters, are herein called "Hennigian analysis," instead of "cladistic analysis." Hennigian analysis provides a corroborated hypothesis of the relative recency of common ancestry, which is then used to nest monophyletic taxa into more inclusive monophyletic groups. Hennigian analysis cannot selectively test the several, alternate, geometric arrangements for only two populations (Fig. 3).

Gaffney (1972a) and Tattersall and Eldredge (1977) contend that the geometry of evolution cannot be tested beyond conventional Hennigian analysis, such hypotheses as are presented in Figure 3 being untestable conjectures. Martin and Whetstone (Ms.) argue that the following criteria will objectively test the various geometrical combinations of evolution: 1) except for evolutionary reversals, which must be assumed to be rare, a direct ancestor must be primitive (plesiomorphic) for every character whereby it differs from daughter populations, 2) a proposed daughter population cannot predate a hypothesized ancestor, 3) a proposed ancestor which postdates or is contemporaneous with a hypothesized daughter population refutes a hypothesis of a single evolutionary lineage without a cladistic event (Fig. 3-1). Despite its geological age, *Emarginachelys* possesses

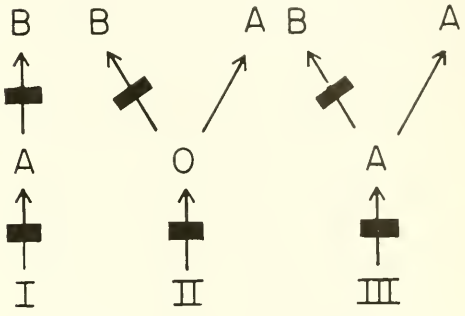

Fig. 3. Alternate hypotheses of phylogenetic linkage between two "taxa." Solid bars represent derived character states. Model II represents the hypothesis that neither "A" nor "B" is ancestral to the other.

many derived features, especially of braincase and plastron, which make unparsimonious any hypothesis of an ancestral position to other known chelydrids.

A thoroughly nested classification presumes coordinate rank of sister taxa. If this concept is used to name each coordinate sister group pair, classifications rapidly become unwieldy and unstable. New names, names of new rank, and a superfluous number of monotypic higher taxa often result (e.g., McKenna, 1975, and Gaffney, 1977). Gaffney (1977), however, argues that "although stability is often considered an important quality of classifications, . . . it is often a spurious and misleading indication of phylogenetic 'truth'." These problems increase markedly with the incorporation of fossil taxa, not because fossil taxa are inherently different, but because many higher taxa must be employed to deal with them.

Patterson and Rosen (1977) suggest a different approach to the classification of

fossils, namely, that "fossil groups or species, sequenced in a classification according to the convention that each group is the (plesiomorph) sister group of all those living and fossil that succeed it, should be called 'plesions.' Plesions may be inserted anywhere (at any level) in a classification without altering the rank or name of any other group. They may bear a categorical name representing any conventional rank, from genus and species upward . . . , these ranks being those already existing in the literature, used only for reference and to avoid ambiguity." I adopt this convention in the classification which follows.

HIGHER PHYLOGENY OF TURTLES

Prior to Gaffney (1975a) most Mesozoic turtles were placed in the "wastebasket" taxon Amphichelydia, thought to be intermediate in structure between living cryptodires and pleurodires. Gaffney presents a convincing shared derived character analysis for a basic cryptodire-pleurodire dichotomy and redistributes most of the taxa previously assigned to the Amphichelydia. The more basic differences between cryptodires and pleurodires are in the trochlear system of the skull for the adductor jaw muscu'ature and the akinetic modifications of the braincase and "palatoquadrate." Cryptodires have a processus trochlearis oticum and a pterygoid brace to the braincase, while pleurodires have a processus trochlearis pterygoidei and a quadrate brace.

Within the Cryptodira, Gaffney recognizes four superfamilies, the Baenoidea, Chelonioidea, Trionychoidea, and the Testudinoidea. In the Trionychoidea he places the kinosternids, dermatemydids, trionychids, and *Carretochelys,* based on the reduction of the stapedial artery and the presence of the "caudifibularis" muscle (Zug, 1971), both assumed to be synapomorphous. Trionychoids also have the costal bones meeting behind the neurals, a reduced postorbital bone, and lack a biconvex 4th cervical vertebra.

If based solely upon the arterial condition and the musculature, a hypothesis of monophyly for these taxa would be questionable. The reduction of the stapedial artery in kinosternids and *Dermatemys* results from enlargement of the palatine artery, while in trionychids and *Carretochelys* it is the result of the enlargement of the pseudopalatine artery (McDowell, 1961; Albrecht, 1967). Neither arterial condition seems intermediate to the other and I suggest that they are nonhomologous. Walker (1973) has interpreted Zug's "caudifibularis" as the dorsal head of the M. flexor tibialis externus that has shifted its insertion from the tibia (the primitive insertion found in most turtles) to the fascia overlying the tibia. This muscle shift is found in all trionychoids, but it is not of such complexity that parallel evolution would be unparsimonious.

Reduced postorbitals are also found in some testudinids and pleurodires but have been acquired independently in these taxa. An elongate (primitive, but often laterally reduced) postorbital is found in all chelydrids, some testudinids (e.g. *Chrysemys scripta*), in most other cryptodires, and in some pleurodires. A reduced neural series is characteristic of most pleurodires but is also assumed to be convergent since some primitive pleurodires have a complete series of neurals (e.g. *Platychelys*). The absence of a biconvex 4th cervical centrum is presumed to be primitive for turtles.

The Chelonioidea as defined by Gaffney (1975a, p. 418, 428) excludes the more primitive members which Gaffney places in this group, the Plesiochelyidae. A more thorough, derived character analysis which attempts to incorporate these turtles is given by Gaffney (1976), who concludes that all chelonioids have a high dorsum sellae, not overhanging the sella turcica as in testudinoids, and which bears a prominent sagittal ridge. An examination of the dorsum sellae of other reptiles reveals that crocodiles, many lizards, some dinosaurs, and *Captorhinus* also have a high, non-overlapping dorsum sellae. DeBeer (1937, p. 256) notes that the dorsum sellae is high in early embryos of *Emys*. This structure even bears a sagittal ridge in *Captorhinus* (see Fox and Bowman, 1966). My initial reaction to these comparisons was to consider the high dorsum sellae of chelo-

nioids as a primitive feature shared by the reptiles cited, but the presence of the low dorsum sellae in baenoids, testudinoids and pleurodires indicates, in the absence of other evidence, that the common ancestor of cryptodires and pleurodires possessed a low dorsum sellae and that the chelonioid structure is a shared, derived character. A discovery that some primitive cryptodires or pleurodires have a high dorsum sellae would refute this hypothesis and support the view that these groups reduced the dorsum sellae independently. Other derived characters in the braincase and forelimbs are shared by the advanced chelonioid taxa, including the Toxochelyidae, to which chelydrids have been allied by some observers (Hay, 1908, p. 27; Zangerl, 1953, p. 267).

The testudinoids form a homogenous group for which I can hypothesize only a single, weak synapomorphy, the biconvex 4th cervical vertebra. Characters which may relate them to other turtles include: 1) the biconvex 4th cervical vertebra—absent in primitive baenoids and "trionychoids," present in all chelonioids in which cervicals are known; 2) loss of mesoplastra—mesoplastra present in baenoids, lost in all other cryptodires; 3) loss of nasal bones—nasals present in primitive baenoids and primitive cheloniods, absent in trionychoids and testudinoids, 4) emargination of temporal region of skull—skull roof well developed in *Proganochelys,* baenoids and chelonioids (except for *Corsochelys*), emarginate in all testudinoids and trionychoids, except *Macroclemys* and *Platysternon.* I suggest that testudinoids and trionychoids form a monophyletic group sharing relatively great temporal emargination and loss of nasal bones, and that their most immediate common ancestor lacked a biconvex 4th cervical. A biconvex 4th cervical is hypothesized to have been independently derived by testudinoids, some baenids and chelonioids. This is not yet a convincing argument, since it is based on characters that seem to be "easily" acquired, but I propose it as a testable hypothesis.

Monophyletic groups within the Testudinoidea may be proposed as shown in figure 4. The Chelydridae, including *Emarginachelys, Chelydra, Protochelydra* and *Macroclemys,* are diagnosed by derived characters as discussed below. Testudinids (*sensu* Romer, 1956) share two, biconvex cervical vertebrae (Williams, 1950), a character not found in other cryptodires, except *Neurankylus* (see Wiman, 1933). Within the Testudinidae, only *Platysternon* and the Emydinae (of McDowell, 1964) have a double articulation between the 5th and 6th cervical centra. The Emydinae are further characterized by the loss of the "batagurine" process and, in more advanced genera, by the reduction of the pterygoid. As a group, the Batagurinae are diagnosed only by primitive characters, although monophyletic complexes occur within the subfamily as defined by McDowell. Advanced testudines share a number of derived characters including: 1) a high, convex shell; 2) alternate constriction and expansion of the costals; 3) thickened epiplastra; 4) expanded coracoid; 5) reduction of phalangeal number; 6) fusion of ventral margins of femoral trochanters; 7) contact of quadrate posterior to incisura collumella auris; 8) depression of the palate in ventral view; 9) ventral processes of the prefrontals far apart (Loveridge and Williams, 1957; Auffenberg, 1974). Many of

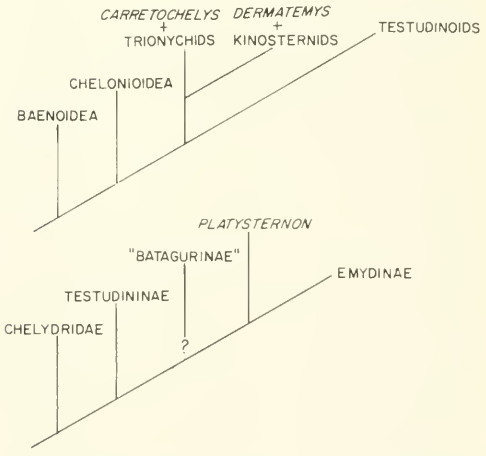

Fig. 4. Hypothesized phylogeny of cryptodiran turtles (top) and testudinoids (below).

these characters are absent in the more primitive living and fossil taxa currently assigned to this group and Auffenberg (1974) suggests that some of the characters may have evolved several times.

In the following discussions, comparisons with baenids and plesiochelyids are based on Gaffney's (1972a, 1976) descriptions and figures unless otherwise noted. Comparisons with *Protochelydra* are based on Erickson's (1973) figures and tables. Terminology of cranial structures follows Parsons and Williams (1961) as illustrated by Gaffney (1972b).

SYSTEMATIC DESCRIPTION

Superfamily TESTUDINOIDEA
Family CHELYDRIDAE
Genus *EMARGINACHELYS* n. gen.

Type species.—*Emarginachelys cretacea* n. sp.

Diagnosis.—Cryptodiran turtle with processus trochlearis oticum and pterygoid brace to the braincase; foramen stapedio-temporale not reduced; nasal bones absent; prefrontals downturned anteriorly; frontals bordering the orbits; the skull roof narrowed above the orbits; otic bridge broad; supraoccipital crest long and low; jugal and postorbital bones elongate; premaxillary "hook" absent; quadrate open behind the stapes; cheek region with some lateral emargination; foramen posterior canalis carotici interni not bordered by basisphenoid; foramen carotico-pharyngeale not enlarged; fossa for attachment of the pterygoideus musculature not extending far anteriorly; triturating surface of maxilla narrow, with a prominent secondary ridge; pterygoid "waist" neither broad, as in *Chelydra,* nor greatly constricted, as in *Macroclemys temminckii;* vomer contacting palatines posteriorly; foramen nervi trigemini and foramen cavernosum small, situated anterior to the dorsum sellae; prootic contacting processus clinoideus laterally; epipterygoid (?) absent; dorsum sellae low, overhanging the sellae turcica; neither foramen caroticum laterale nor foramen anterior canalis carotici interni enlarged; one biconvex cervical vertebra; costal bones not meeting behind the neurals; no serration of the carapace posteriorly; supramarginal scutes absent; carapace weakly keeled medially, costals with parallel ridges; peripherals unsculptured; no carapacial fontanelles; nuchal bone with long, costiform processes; plastron cruciform, ligamentously attached to the carapace; entoplastron reduced, but not "T" shaped; right and left sides of plastron in contact, but not sutured together; thecal process on the ilium; pectineal processes of the pubis not laterally expanded; pubis and ischium separated medially.

EMARGINACHELYS CRETACEA n. sp.

Diagnosis.—Same as for the genus.

Holotype.—KUVP 23488: carapace; plastron; skull lacking lower jaw; right stapes, posterior horn of hyoid; right forelimb and girdle lacking phalanges of digits IV and V; left forelimb and girdle lacking pisiform and distal half of metacarpal V; left hindlimb and girdle lacking most of digits I and V and the distal phalanx of digit IV; right ilium; cervicals 3-7; anterior half of cervical 8; caudals 1-3.

Horizon and Type Locality.—Hell Creek Formation (Upper Cretaceous); Garfield County, Montana; SW ¼ NW ¼ S. 35, T. 21 N., R. 37 E.

MORPHOLOGIC AND COMPARATIVE DESCRIPTION

Skull, Dorsal View (Fig. 5, 6).—The skull roof is composed of the frontal, prefrontal, parietal, and postorbital bones. Nasal bones are absent. The prefrontals are strongly downturned anteriorly, unlike *Chelydra* and *Macroclemys.* The descending process of the prefrontal forms the anterior wall of the fossa orbitalis and the posterior wall of the fossa nasalis. The dorsal portion of the fissura ethmoidalis is not broadly expanded as in testudines or *Adocus,* but resembles the condition in *Chelydra* and emydines. The foramen supraorbitale is preserved on the right side and is indistinguishable from that of *Chelydra.*

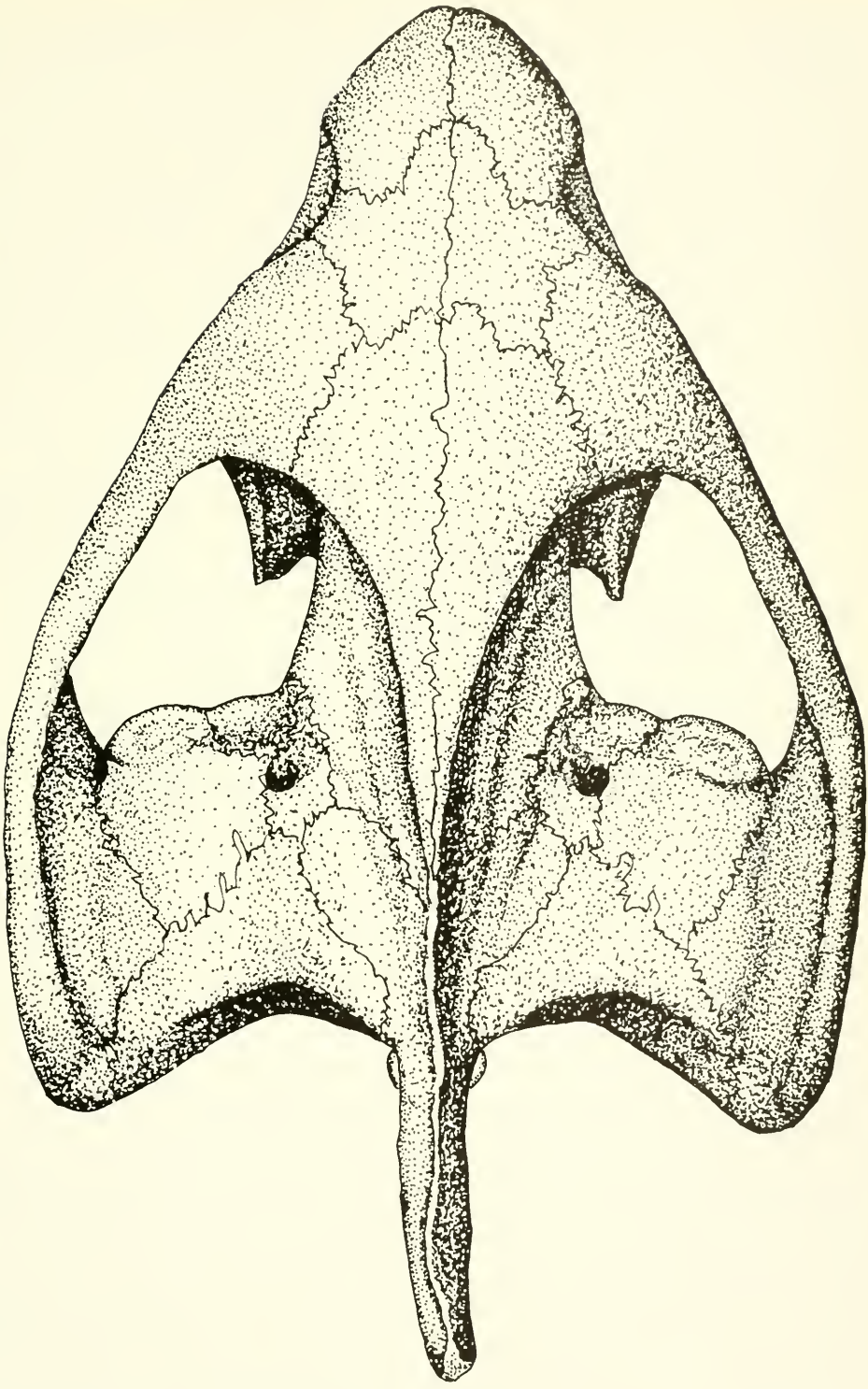

Fig. 5. *Emarginachelys cretacea* (KUVP 23488), restoration of skull in dorsal view. Skull length (condyle to tip of snout) is 77 mm.

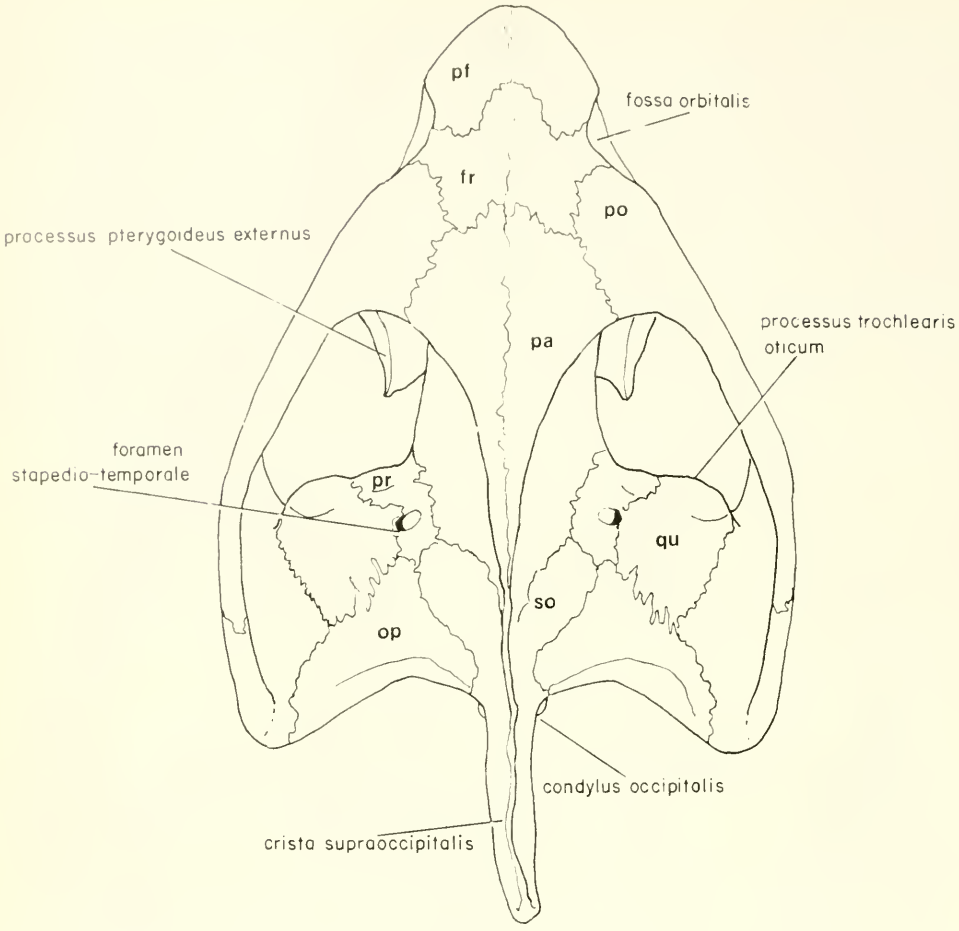

FIG. 6. Key to Figure 5.

TABLE 1: Skull Measurements for Holotypes of *Emarginachelys* and *Protochelydra*.

	Emargi-nachelys	*Proto-chelydra*
Skull length (condyle to tip of snout)	77.1 mm	77.8
Maximum skull width	57.0	69.8±
Width across quadrates	52±	68
Width of posterior alveolar surface	10.1	16.5
Width of snout at anterior end of orbit	18.7	20±
Width of snout at posterior end of orbit	31.2	38.2±
Anterior snout height	13.5±	14
Distance from anterior wall of orbit to nasal notch	6.4	6.2
Distance from posterior rim of orbit to anterior margin of temporal emargination	11.4	15.7

The frontals are relatively large and make up a large portion of the skull roof. The prefrontal and postorbital bones do not meet above the orbits. This allows the frontal bones to contact the dorsal margins of the fossa orbitalis. Contact of the frontal bones with the orbits is a primitive feature for cryptodires that is lost in other chelydrids and in some other testudinoids. *Dermatemys* and *Trionyx* have the primitive relationship between the frontal bones and the orbit.

Compared to those of *Chelydra,* the parietals of *Emarginachelys* are much reduced by the extreme posterior emargination of the temporal region. Gaffney (1975b) theorized that such emargination was primitive for the Chelydridae. The fully-roofed condition, is however, almost certainly primi-

tive for the Cryptodira as judged by the temporal regions of baenoids, chelonioids, some pleurodires, and *Proganochelys*. Gaffney's hypothesis is supported by presence of the emarginate condition in the temporal region of the Upper Cretaceous *Emarginachelys,* and I interpret the expanded temporal region of *Macroclemys* as an evolutionary reversal. The skull roof bones of *Emarginachelys* are not strongly sculptured as in *Chelydra*. The frontals extend as far forward on the skull midline as the anterior margin of the orbits. Above and between the orbits, the skull roof is constricted as in *Chelydra* and *Protochelydra*.

The otic bridge, which covers the otic region dorsally, is longer antero-posteriorly than in any other chelydrid or *Platysternon*. In this respect, *Emarginachelys* resembles trionychoids and primitive emydines, and I assume that a broad otic bridge is primitive for testudinoids. The foramen stapediotemporale is situated between the prootic and the quadrate. The sutural contacts between the squamosal, quadrate, and opisthotic bones are partially obscured by cracks, but are interpreted to be as in Figure 6. The supraoccipital crest is long, but is lower than in *Chelydra* or *Macroclemys*.

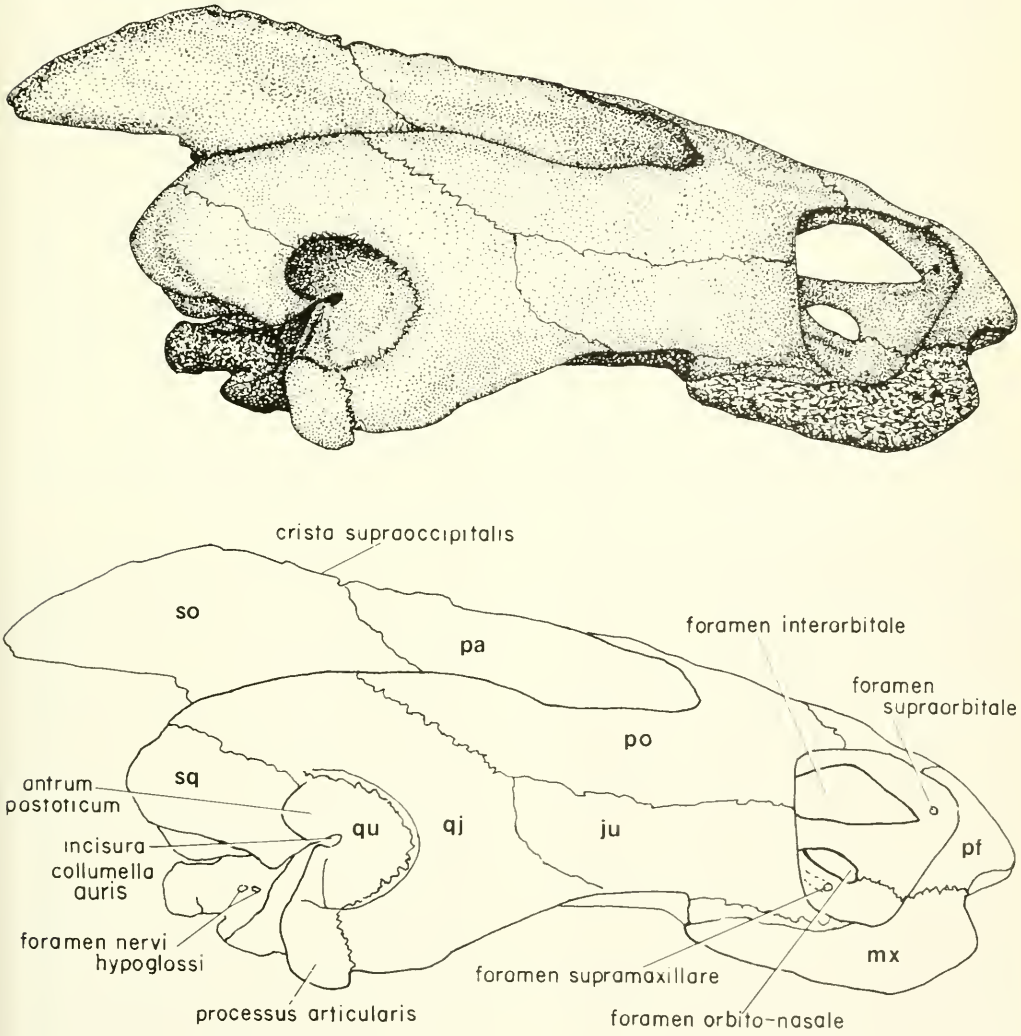

Fig. 7, 8. Fig. 7—Restoration of skull in lateral view. Skull length is 77 mm. Fig. 8—Key to Figure 7.

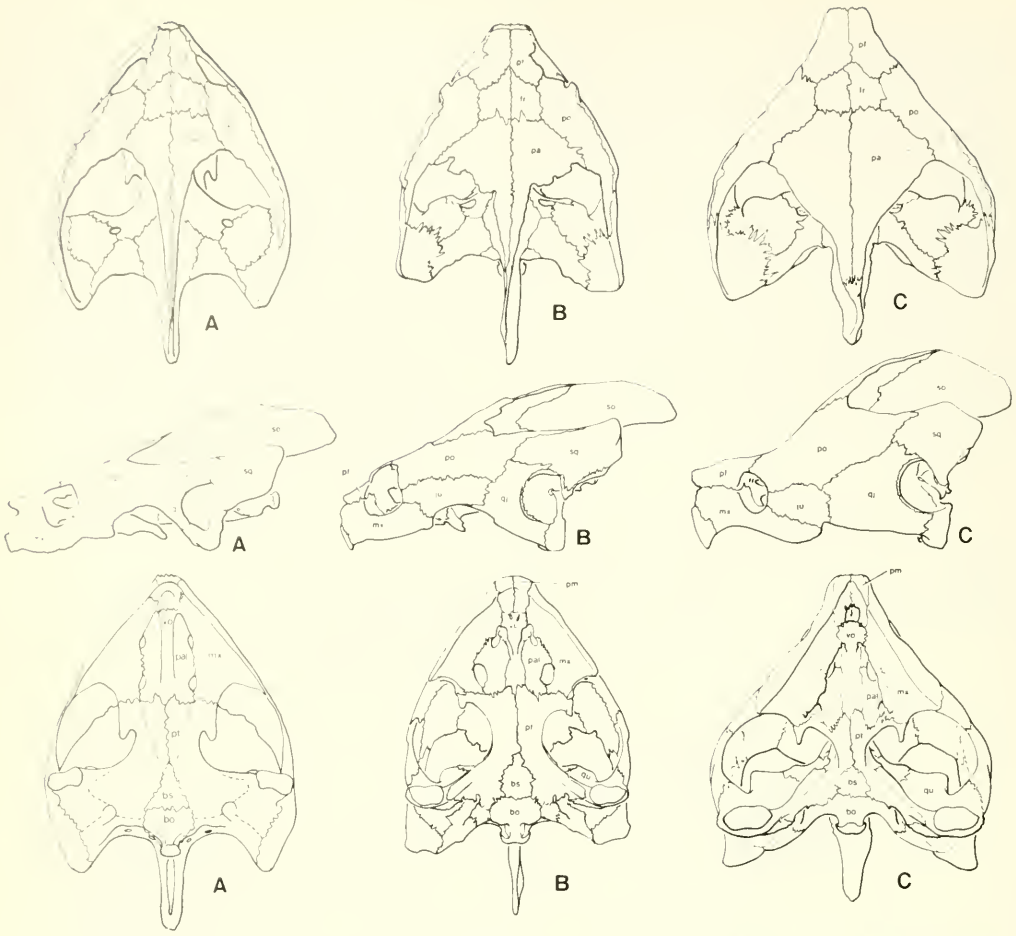

FIG. 9. Skulls of other chelydrid turtles: A) *Protochelydra,* B) *Chelydra,* C) *Macroclemys* (A after Erickson 1973 and Gaffney 1975b; B, C after Gaffney 1975b). Not to scale.

Lateral View (Fig. 7, 8).—The orbital rim is large and prominent, bounded by the prefrontal and maxillary anteriorly and by the jugal and postorbital posteriorly. The infraorbital canal and foramen orbital-nasale are situated approximately as in *Chelydra.* The orbit is partially walled posteriorly by medial extensions of the jugal and maxillary and by a lateral extension of the palatine. A well-developed, posterior wall for the fossa orbitalis is not found in *Chelydra* or *Platysternon,* but is found in some kinosternids and in *Macroclemys.* In *Emarginachelys,* the inframaxillary artery entered this wall anteriorly and exited through the foramen palatinum posterius after passing through a short canal. The foramen palatinum posterius is small, unlike that of *Chelydra,* but like the foramen of *Macroclemys.*

The premaxillae are not produced into a "hook" as they are in other chelydrids, kinosternids, some testudines, and *Platysternon.* The maxillae are not constricted towards the midline. The jugal and postorbital are relatively long as in all chelydrids. Gaffney (1975b) hypothesized that a relatively long jugal was primitive for the Chelydridae. This hypothesis was based on the presence of a long jugal in the geologically old *Protochelydra* (Fig. 9), since almost all cryptodires have relatively short jugals. The presence of a long jugal in *Emarginachelys* does support this hypothesis, even though this bone is substantially shorter than in *Protochelydra.* The shorter jugal in *Macroclemys temminckii* is interpreted as a

reversal. The postorbital bone is long in chelonioids, baenoids, and chelydrids and this condition is probably primitive for cryptodires. In the "cheek" region, *Emarginachelys* is only slightly emarginate, unlike *Protochelydra* and *Chelydra,* but similar to *Macroclemys.* This does not support Gaffney's (1975b) hypothesis of a primitively emarginate cheek region for chelydrids. The weakly emarginate condition also occurs in the primitive baenoids, *Trinitichelys* and *Naomichelys*, and in *Platysternon, Damonia, Proganochelys, Desmatochelys* and cheloniids. I suggest that the relatively-great, lateral emargination of *Chelydra* and *Protochelydra* may be a shared, derived feature for these turtles.

The incisura columella auris of the quadrate is narrowly open posteriorly, unlike the quadrates of all other chelydrids and most testudines. The open condition is probably primitive, since it occurs in most cryptodires (including emydines), and in most sauropsid reptiles. The processus articularis of the quadrate is much shorter in *Emarginachelys* than in *Chelydra.*

Ventral View (Fig. 10, 11).—The tuberculum basioccipitale is accentuated by the strong depression of the basioccipital to accommodate the insertion of the rectus capitis muscle. There is little postero-lateral expansion of the pterygoid, leaving the otic region more open ventrally than in other chelydrids or *Dermatemys.* The processus interfenestralis and the prootic are exposed ventrally in the fenestra postotica. The ventral margin of the foramen posterior canalis carotici interni is formed by the pterygoid; the dorsal margin by the prootic.

The right stapes is preserved more or less in place. The footplate of the stapes is flattened and the shaft does not extend from the center of the footplate. Both plesiochelyids and other chelydrids have a similar stapedial morphology, a condition which I interpret as primitive. *Dermatemys* and kinosternids have conical footplates that are symmetrical about the shaft of the stapeidal rod (McDowell, 1961), an additional synapomorphy uniting these taxa.

The ventral surface of the basisphenoid extends only slightly beyond the mandibular condyles anteriorly, as in *Protochelydra* and some emydines. *Macroclemys, Chelydra,* baenids and plesiochelyids generally have the basisphenoid extending farther beyond the mandibular condyles. I am uncertain which condition is primitive for testudinoids. On the pterygoid brace to the braincase, lateral to the basisphenoid and posterior to the fossa temporalis inferior, are depressions for the attachment of the pterygoideus musculature like that of many emydines (e.g. *Graptemys*), *Macroclemys,* baenids, and plesiochelyids. I suggest that a posterior depression for the pterygoideus musculature is primitive and that the extension of the depressed surface anterior to the area of the processus pterygoideus externus is a derived character shared by *Chelydra* and *Protochelydra* (see Erickson's figure 1).

The skull of *Emarginachelys* is narrower in many proportions than is that of *Chelydra* (compare Figs. 9 and 10). The distance between the quadrates is relatively less, as is the width of the pterygoid waist, the distance between the processi pterygoidei externi, and the distance between the postero-medial margins of the triturating surfaces of the upper jaws. The processi pterygoidei externi of *Emarginachelys* are only slightly extended ventrally. The triturating surfaces of the maxillae are relatively narrow and bear a pronounced median ridge on the posterior portion, similar to that of some testudinids. Among cryptodires, this type of ridging is found only in some testudinids *(sensu lato), Dermatemys,* and *Adocus,* and seems to be correlated with herbivory. Since ridging is lacking in kinosternids and trionychids, which share a number of derived characters with *Dermatemys,* the presence of midline maxillary ridges cannot be used to unite *Emarginachelys* with dermatemydids.

The foramen palatinum posterius is small, unlike this foramen in *Chelydra.* It is situated near the postero-medial corner of the maxilla. The labial ridge of the maxilla is straight, unserrated and prominently raised from the level of the triturating surface. The labial ridge is continued across the midline by the premaxillary bone. There is no premaxillary "hook," a derived feature shared by other chelydrids, and no median recess

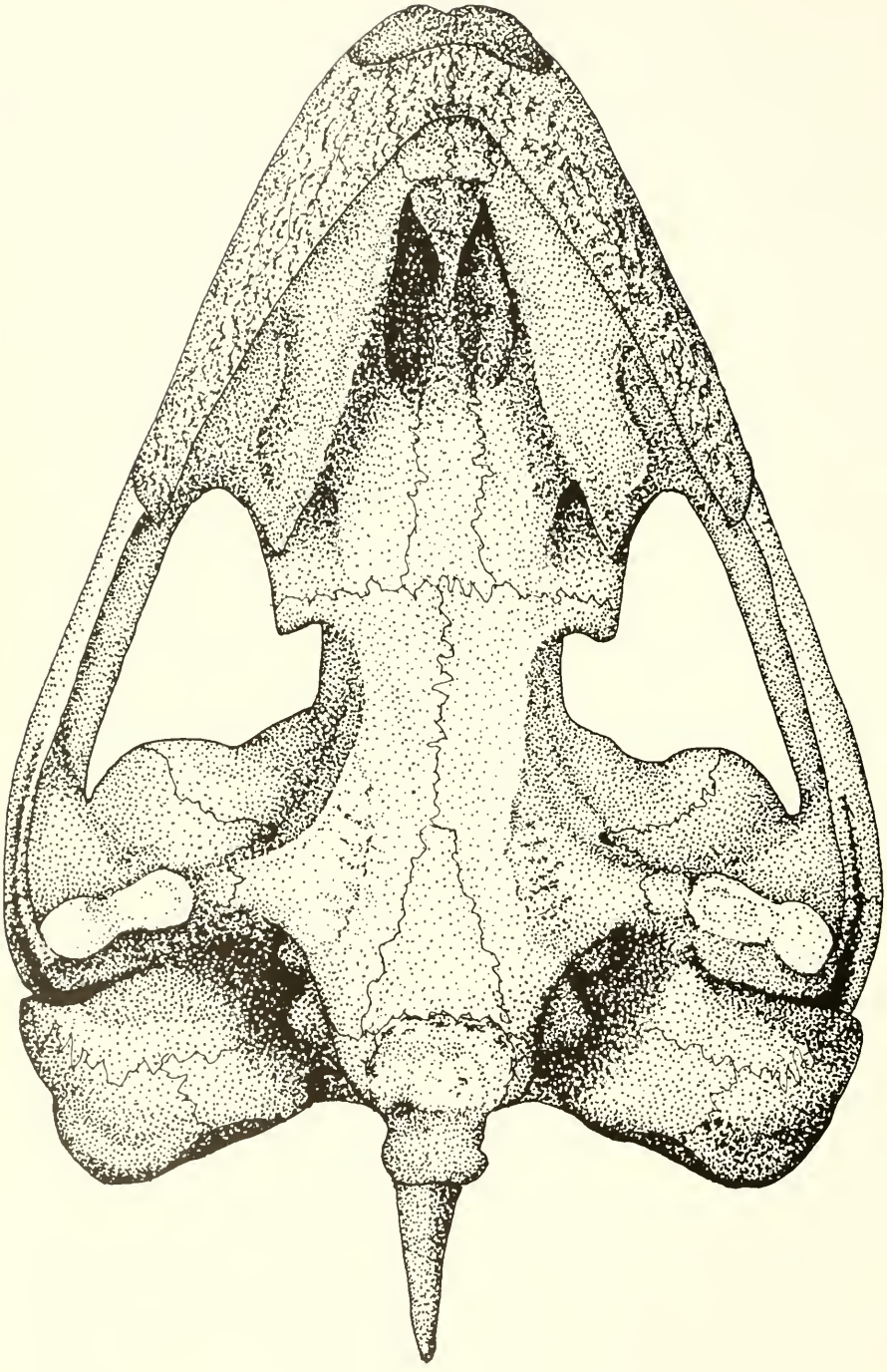

FIG. 10. Restoration of skull in ventral view. Same scale as Figure 5.

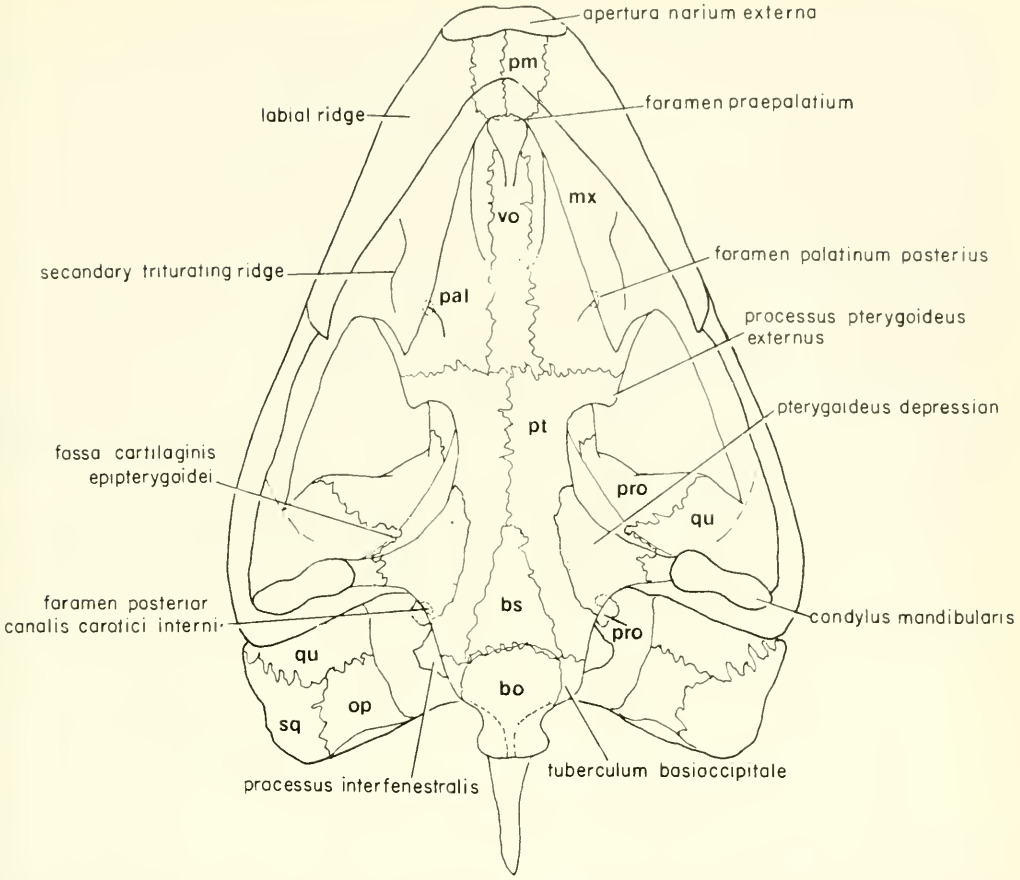

Fig. 11. Key to Figure 10.

exists in the premaxillary. A median recess is present on premaxillae of emydines and batagurines. The triturating surface of the maxilla narrows anteriorly and terminates at the sutural contact between the vomer and the maxilla. The vomer and premaxillae bear the paired foramina praepalatina. As in all chelydrids, the vomer contacts the palatines posteriorly and is not crested ventrally.

Braincase (Fig. 12).—The parietals form most of the side wall of the braincase. The foramen nervi trigemini is small and is situated dorsal and anterior to the dorsum sellae. Its margins are formed mostly by the prootic internally and mostly by the parietal externally. There is a distinct fossa cartilaginis epipterygoidei, but there appears to be no independently ossified epipterygoid. It is also possible that I have incorrectly interpreted, as cracks, the sutures which delimit this bone. The quadrate is narrowly excluded from the foramen nervi trigemini, but forms the posterior border of the fossa cartilaginis epipterygoidei. The descending processes of the parietals are broad. In this respect and in the dorsal position of the foramen nervi trigemini, *Emarginachelys* resembles *Dermatemys* and is unlike *Chelydra* and *Macroclemys*.

The structure of the floor of the braincase is difficult to interpret, due to both its uniqueness and to post-mortem damage. The left side of the braincase anterior to the dorsum sellae is considerably crushed and the right side posterior to the dorsum sellae has been damaged by root growth into the skull. The foramen cavernosum is situated anterior to the dorsum sellae, just ventral to the trigeminal foramen. The anterior placement of the foramen cavernosum is, to my knowledge, unique among turtles. The situation is apparently the result of the union of the

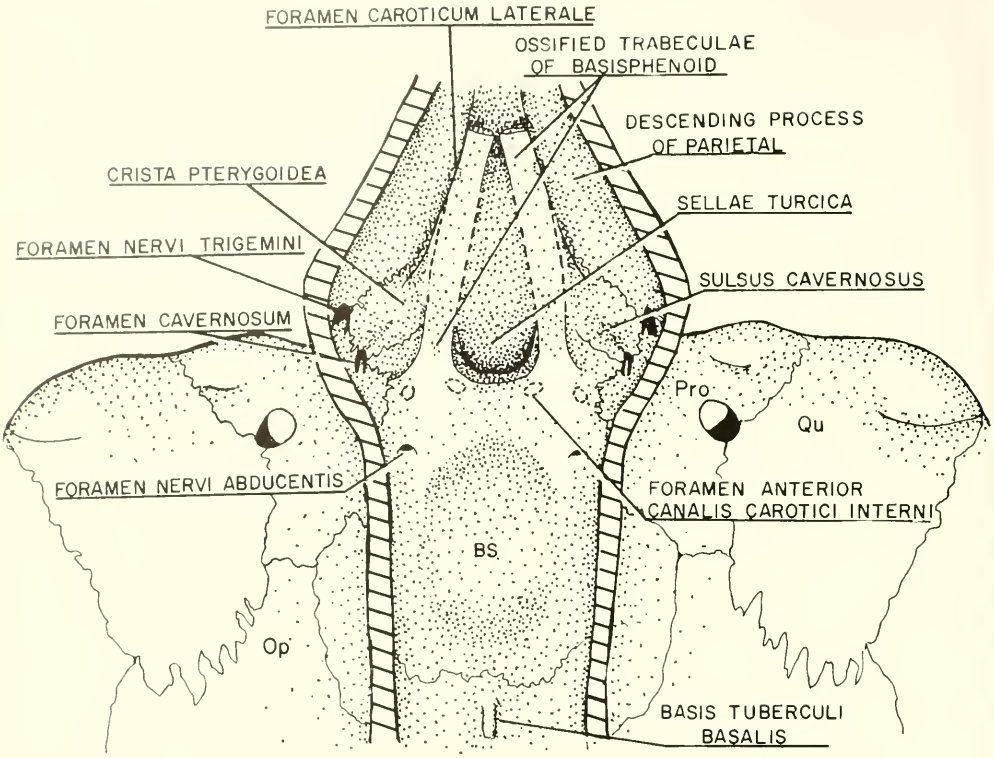

FIG. 12. Restoration of braincase in dorsal view.

processus clinoideus with the prootic which is anteriorly expanded medial and dorsal to the area normally occupied by the sulcus cavernosus. The dorsum sellae is low and overlaps the floor of the sellae turcica. The anterior internal carotid foramina are situated beneath the shelf of the dorsum sellae and are closer together than in *Chelydra*. Part of the trabecula of the right side is preserved; beneath it the lateral carotid foramina can be located with probes. They are close in size to the anterior internal carotid foramina, but direct measurement is impossible. The crista pterygoidei is short and bears the sulcus cavernosus as it rises toward the foramen cavernosum.

Cervical Vertebrae.—Most of the third through eighth cervical vertebrae are preserved. The cervical, central articulations may be represented by Walther's (1922) formula as (3(4)5)6 7 8. This is comparable to the cervical central pattern of *Macroclemys* and *Chelydra*. With only rare exceptions, these turtles have the patterns (2(3(4)5)6)7)8) and (2(3(4)5)6 7 8) (Williams, 1950). The eighth cervical of *Emarginachelys* is not biconvex as in emydines, batagurines, testudines, and *Platysternon*. A biconvex, fourth cervical is a derived character which occurs only in some eucryptodires (sensu Gaffney), with the possible exception of *Neurankylus*. The cervical centra of *Emarginachelys* are much shorter than those of recent chelydrids with a comparably sized carapace. Otherwise the centra are morphologically similar to those of *Chelydra* and *Macroclemys*.

Carapace and Plastron (Fig. 13).—The carapace and plastron of *Emarginachelys* shows features absent in other chelydrids. The bones of the carapace are thick, especially the neurals and peripherals. There is no emargination anteriorly and scalloping posteriorly. There are 11 pairs of peripherals, 8 pairs of costals, 8 neurals, 2 suprapygals, and one nuchal. The neurals are longer than

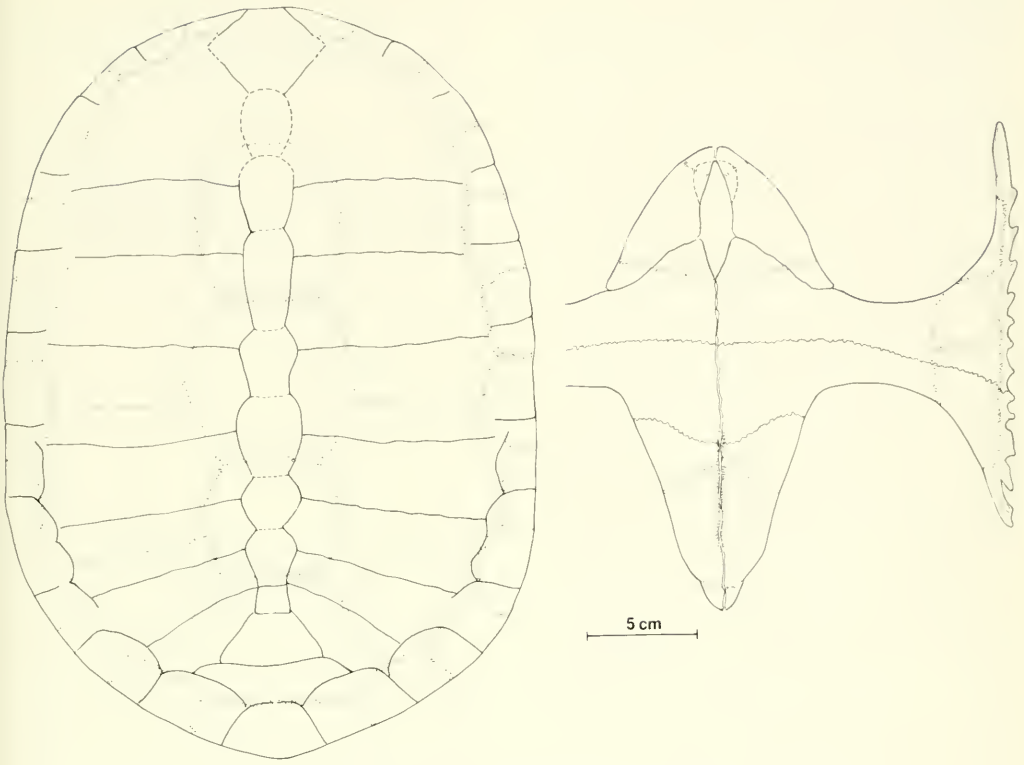

Fig. 13. Partial restoration of carapace and plastron.

wide and narrow sharply anteriorly. The impression of the most anterior vertebral scute cannot be discerned. The impressions of the remaining vertebrals are about as wide as they are long and approximately square in outline. There are no supramarginal scutes as are found in *Macroclemys temminckii*.

A low, median keel extends from the 4th neural posteriorly to the base of the posterior suprapygal. Auxillary ridges extend from the posterior of the 4th through 7th neurals and diverge anteriorly and laterally, terminating after a short distance. Costals 5 and 6, on the inferior half, and costals 4 and 5, on the superior half, are strongly sculptured with parallel ridges similar to the costal sculpture of *Pseudemys*. Costals with similar sculpture from the Upper Cretaceous Lance Formation were described by Estes (1964). These may belong to *Emarginachelys*, rather than to *Neurankylus* as suggested by Gaffney (1972a). There is no sculpture on the peripherals. Cross sections of several peripherals are shown in Figure 14. Peripherals 4, 5 and 6 are elongated in the ventral direction for the attachment of the plastron. There is a lateral "keel" on these peripherals that merges on peripherals 3 and 7 with the ventral margin of the carapace. Pits in the ventromedial margins of the peripherals are directed inward and downward for reception of the digitate lateral projections of the plastron. The 4th and 7th peripherals are the more deeply pitted while the 5th and 6th are shallowly pitted at the ventro-medial margin. The posterior peripherals are tapered as in *Dermatemys*.

The broad prezygapophyses of the first dorsal vertebra curve downward and outward to allow vertical flexure of the neck. The ventral surfaces of the succeeding dorsal vertebrae are not flattened as in *Chelydra*. The 2nd, 3rd, and 4th dorsals are ventrally keeled as in *Dermatemys*, but the more posterior dorsals are ventrally rounded. The 9th and 10th dorsals are procoelous, the 10th

strongly so. The ribs of the 10th dorsal are free. Ribs of the three sacral vertebrae are modified for a support for the pelvic girdle, as in *Chelydra*. The distal rib-heads of the costals fit into "V" shaped notches in the peripherals. There appears to have been no ventral closure of the peripherals under the distal rib ends. There are no fontanelles between the costal and peripheral plates as occurs in other chelydrids and in some toxochelyids.

The plastron is cruciform, with broad antero-posterior extensions of the hyo- and hypoplastra for the ligamentous attachment with the carapace. A ligamentously attached "buttress" extends from the antero-lateral prong of the hyoplastron along the medial margin of the peripherals and attaches in a pit at the juncture of the 3rd and 4th peripherals, the point of termination of the costiform process of the nuchal bone. The anterior margin of the carapace is thus braced by a ring of bone extending anteriorly from the right 4th peripheral across the anterior margin to the left 4th peripheral. I am not sure of the functional advantages of such a bony support, but I suspect that it is associated with the reduced, ligamentously attached plastron in a heavy bodied, semi-aquatic turtle.

The entoplastron is not "T" shaped as in other chelydrids, but is roughly triangular in outline, with a narrowly tapered posterior tip. It is articulated to the surrounding plastral bones by a kinetic squamous articulation (Fig. 13). Some of the anterior portion of the entoplastron extends laterally over the dorsal surface of the epiplastra and is not visible in ventral view (Fig. 13). The hyo- and hypoplastra are strongly sutured together with most of the plastral bridge being formed by the hyoplastron. The epiplastra are broad compared to those of other chelydrids. The epiplastra articulate with the hyoplastra by convexo-concave "joints" and the right and left epiplastra do not suture together at the midline. The remaining plastral elements articulate with their counterparts of the other side in a loose kinetic articulation. This plastral morphology is unique and highly derived, differing from that of sea turtles. Plastral kinesis allowed free movement of the plastron by flexure perpendicular to the antero-posterior axis. The strong sutures between the hyo- and hypoplastra allowed no kinesis at the midline perpendicular to a lateral axis.

The impressions of the three inframarginal scutes and the gular, humeral, and anal scutes are preserved. They are essentially as in *Macroclemys*. Impressions of the remaining plastral scutes cannot be determined.

Analysis of Shell Morphology.—The shell of *Emarginachelys* differs from that of other chelydrids in the absence of plastral and carapacial fontanelles. In this respect it resembles most adult testudinids (sensu Romer), dermatemydids, baenids, some kinosternids and some *Plesiochelys* (Bram, 1965). I interpret shell reduction by fontanellization as a shared, derived feature for *Protochelydra* (lacks plastral fontanelles), *Chelydra,* and *Macroclemys*. The *Emarginachelys* entoplastron and xiphiplastra are reduced, relative to the primitive condition of cryptodires, but not as reduced as in *Chelydra* and *Macroclemys*. I interpret the "T" shaped entoplastron, reduced epiplastra, and serrated carapacial margin as further synapomorphies uniting *Protochelydra, Chelydra* and *Macroclemys* and the further reduction of the xiphiplastra as derived features shared by *Macroclemys* and *Chelydra*. If *Protochelydra* and *Chelydra* share a common ancestor not shared by *Macroclemys,* as suggested here, then reduced xiphiplastra and plastral fontanelles would be hypothesized to be derived in parallel.

The cruciform plastron and long costiform processes on the nuchal bone are also found in kinosternids and are particularly well developed in *Staurotypus*. These features, plus the presence of a single, biconvex cervical vertebra, were used by Williams (1950, whose classification was followed by Romer, 1956) to unite chelydrids and kinosternids into a single family. Since these features are absent in *Dermatemys,* which shares a derived cranial artery pattern with kinosternids (McDowell, 1961; Albrecht, 1967; Gaffney, 1975a), I suggest that the costiform process and the cruciform plastron were independently derived in kinosternids and chelydrids. The 4th cervical is biconvex in chelydrids while other cervicals are bioconvex in kinosternids and *Dermatemys*.

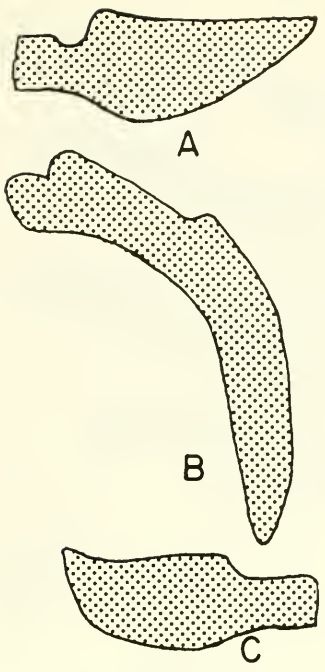

Fig. 14. Semi-diagrammatic cross sections of peripheral bones: A) 9th right, B) 5th right, C) 2nd right. Natural size.

Plastral "buttresses," extensions of the plastron which suturally contact the costals, occur in many pleurodires, baenoids, dermatemydids, and testudinids and are assumed to be primitive for cryptodires. If the long, anterior extensions of the hyoplasta of *Emarginachelys* represent a reduced buttress, then the complete loss of a buttress would be a synapomorphy uniting other chelydrids. Ligamentous attachment of the plastron to the carapace is a derived feature found in all chelydrids, some emydines, *Platysternon,* and *Claudius* among non-chelonioid cryptodires. Since sutural attachment, the plesiomorphous condition, occurs in most testudinids (sensu lato), *Dermatemys,* and kinosternids, I regard ligamentous plastral attachment as examples of parallelism for chelydrids and these other taxa.

Shell morphology has been used (e.g. Hay, 1908; Zangerl, 1953) to suggest a close relationship for chelydrids and toxochelyids. These taxa share the cruciform plastron, "T" shaped entoplastron, ligamentous attachment of carapace to plastron, costo-peripheral fontanelles, and plastral fontanelles, all derived characters for cryptodires. Gaffney (1975a, 1976) suggests that this shell reduction is convergent.

The toxochelyid braincase indicates clearly the affinities of toxochelyids with the plesiochelyids and other chelonioids, as proposed by Gaffney. Derived features of the *Toxochelys* braincase which are shared by some, or all, of the chelonioids, but not by chelydrids, include: 1) a high, crested dorsum sellae that does not overlap the sella turcica (see discussion above); 2) approximated internal carotid arteries; 3) fusion of the ossified trabeculae with reduction of the sellae turcica. The taenia intertrabecularis (see Nick, 1912) may be present as a keel atop fused trabeculae of toxochelyids (Whetstone and Stewart, Ms.). The shell morphology of *Emarginachelys,* which I regard as the most primitive chelydrid, supports Gaffney's hypothesis of convergent shell reduction for chelydrids and toxochelyids, since *Emarginachelys* lacks most of the shell reduction found in later chelydrids or in toxochelyids.

Pectoral Appendages (Fig. 15, 16).—The left and right forelimbs are preserved essentially as they were articulated in life. The left forefoot lacks only the pisiform bone and the proximal half of the fifth metacarpal. Except for the structure of the intermedium, the morphology of the forelimb compares closely with that of adult chelydrids—the metatarsals and phalanges are relatively short and broad; the phalangeal formula is 2-3-3-3-3; the centralia are fused. The intermedium is wedge shaped, extending medially onto the distal surface of the *radius* (Fig. 15). To my knowledge, this carpal morphology is unique to *Emarginachelys.*

The humerus is similar to that of *Chelydra.* It is strongly "S" shaped, with the neck extending outward from the distal part of the shaft at an angle (angle "alpha" of Zangerl, 1953) of about 90 degrees. Its head is elliptical, with a prominent, lateral shoulder. The humeral shoulder of *Chelydra* and *Protochelydra* is poorly-defined while that of *Macroclemys* and *Emarginachelys* is prominent. There is a well-defined, intertrochanteric fossa immediately behind the head. The shaft of the humerus is massive, unlike the slender

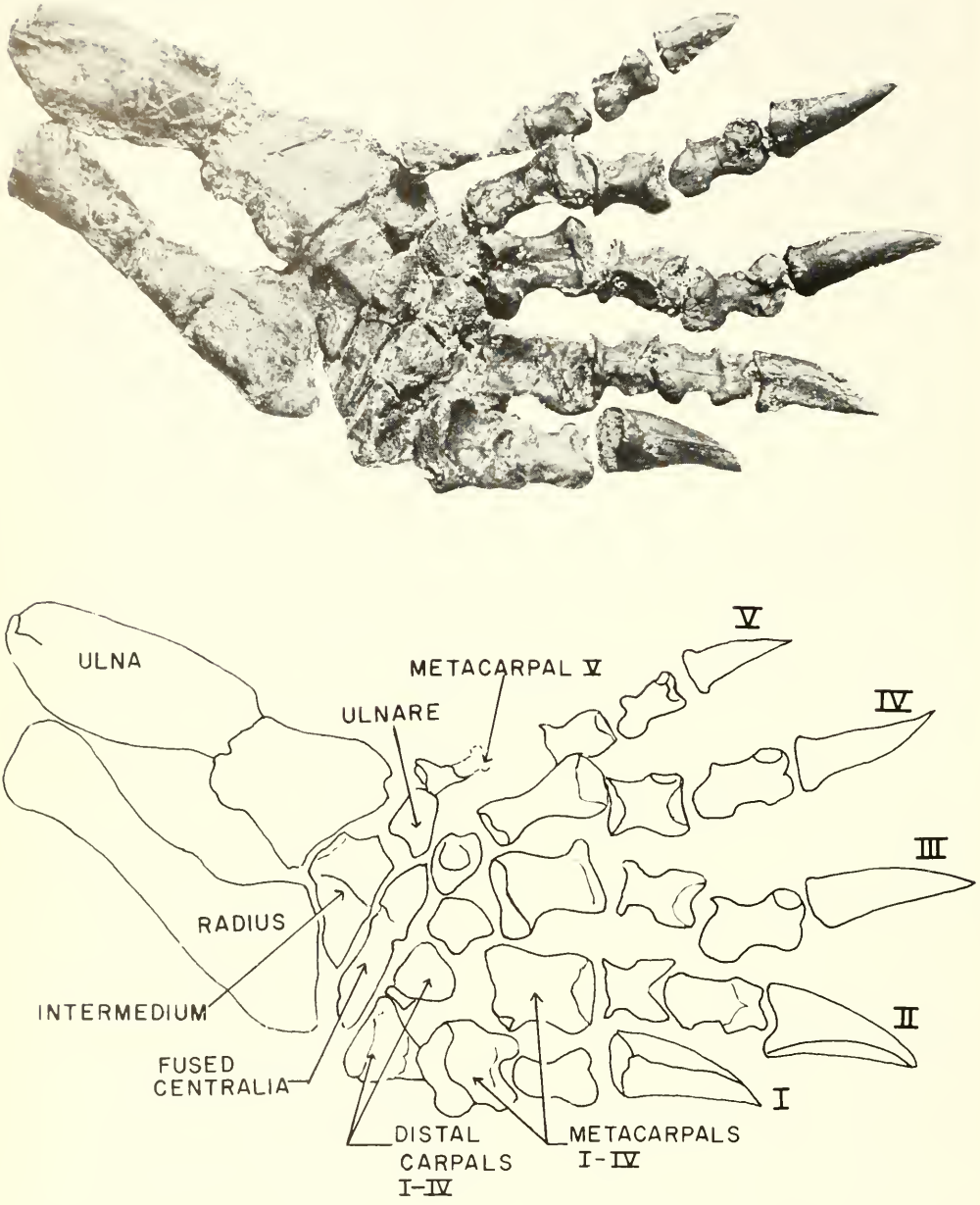

FIG. 15. Left forefoot, radius and ulna. Natural size.

humeri of emydines and *Platysternon*. Distally the shaft expands and bears two stout condyles.

Pectoral Girdle (Fig. 17)—As in all living turtles, the pectoral girdle is a three-pronged structure with postero-medial, medial and dorsal processes. The pectoral girdle compares closely with chelydrids except that the coracoid is less expanded than in *Chelydra*, and the ventro-medial process of the scapula is more massive.

Pelvic Appendages (Fig. 15, 18).—The left

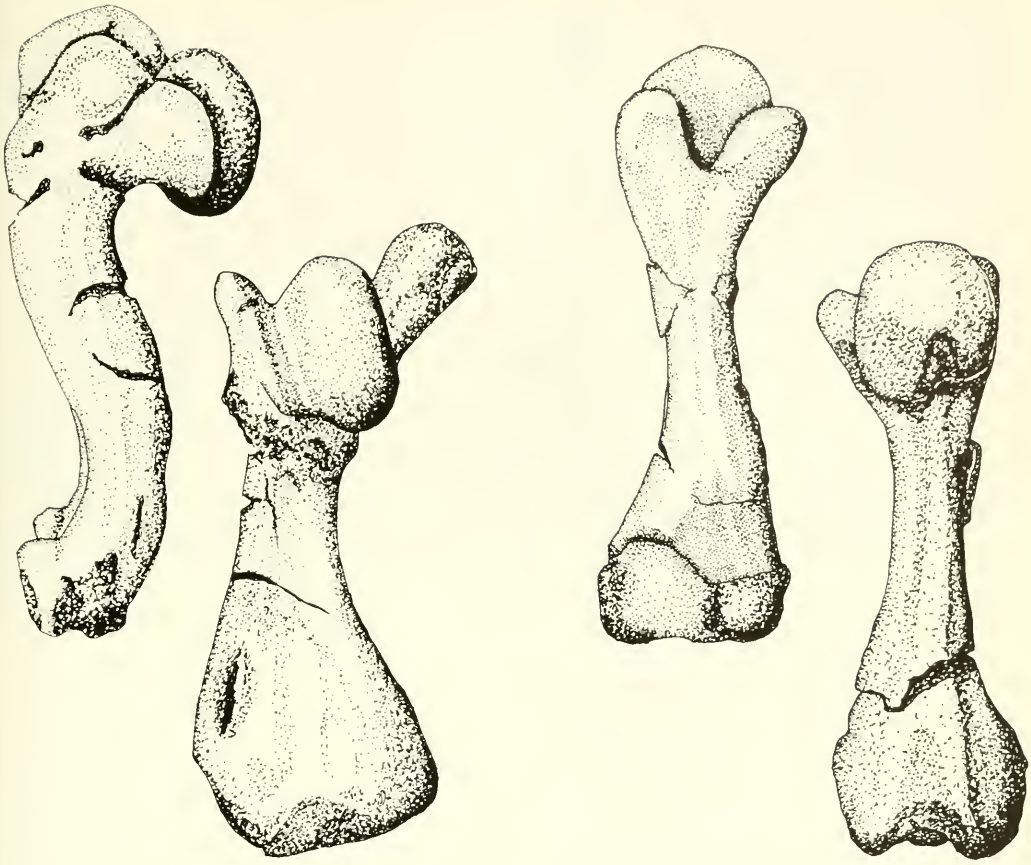

Fig. 16. Left—Lateral and dorsal aspect of left humerus; Right—Ventral and dorsal aspect of left femur. Natural size.

hind limb and the left half of the pelvic girdle are well preserved. The left foot lacks most of digits I and V. As far as can be determined, the phalangeal formula is the same as in *Chelydra*. Of the tarsals, the astragalus and calcaneus are fused; a bump on the distal edge of the astragalus probably represents the fused centrale. The astragalus, calcaneus, and centrale are usually well fused in adult chelydrids, but are sometimes discernible or separate in juveniles (cf. Zug, 1971).

The femur is similar in size and general morphology to that of *Chelydra*. The femoral trochanters are more massive than those of *Chelydra,* with constriction of the intertrochanteric fossa. The fossa is partially enclosed ventrally by a low ridge which connects the distal borders of the trochanters. There is much greater curvature in the shaft than in *Macroclemys* or *Chelydra*. The distal condyles are strongly produced from the ventral surface.

Pelvic Girdle (Fig. 19).—The ilium is strongly inclined posteriorly; at the dorsal end it expands into a rugose surface which served for ligamentous attachment of the pelvis to the carapace. There is a well-developed, thecal process on the anterior margin. Among living cryptodires studied by Zug (1971), only kinosternids have the thecal process on the ilium. If the presence of this process is considered synapomorphous, *Emarginachelys* might be presumed to share a common ancestor with kinosternids and *Dermatemys* that is not shared by chelydrids. I do not accept this interpretation. As discussed above, the cranial circulation of *Dermatemys* and kinosternids is unique and presumably synapomorphous. If a close relationship with *Emarginachelys* exists, the *Dermatemys* ossified shell and the

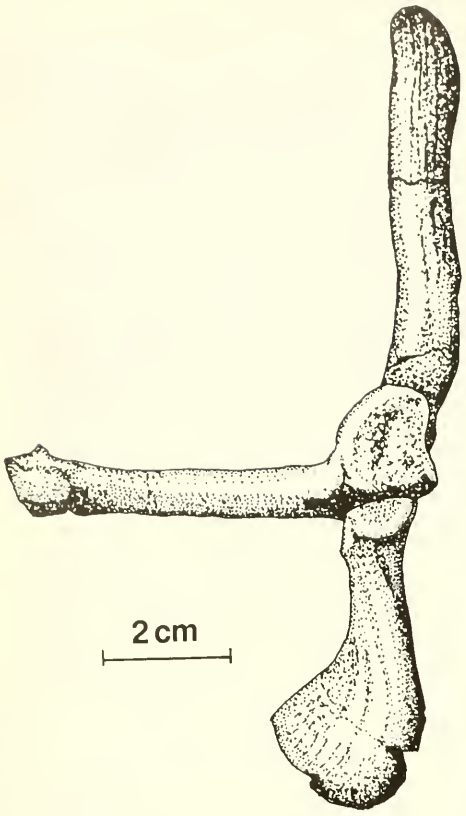

FIG. 17. Left scapulocoracoid in anterior and slightly ventral view.

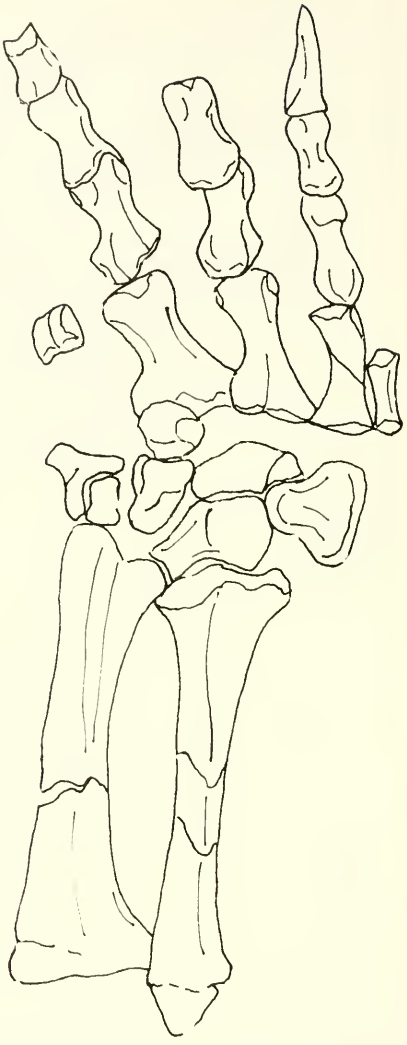

FIG. 18. Left hindfoot, tibia, and fibula. Natural size.

ilium without a thecal process would be hypothesized as evolutionary reversals, or the reduced plastron and ligamentous plastral attachment of *Emarginachelys* would be hypothesized as convergence with chelydrids. *Emarginachelys* also has the costals not meeting behind the neurals, a biconvex 4th cervical, an elongate jugal, and non-divergent pectineal processes (see below). I prefer to regard the thecal process as independently acquired for kinosternids and *Emarginachelys*. A similar process occurs on ilia of some *Toxochelys* and of *Chisternon*, a baenid.

The pubis is narrower medially than in *Chelydra*. It is notched antero-medially for the insertion of the epipubic cartilage. Anterolaterally the pubis bears a process, the pectineal process, which was attached to the plastron by ligaments. Zug (1961) shows that only *Macroclemys* and *Chelydra* among living cryptodires have the pectineal process parallel to each other and to the sagittal plane (Fig. 20). I interpret this as a synapomorphy for advanced chelydrids. The pubis of *Protochelydra* is not known. The *Emarginachelys* pelvis is intermediate between other cryptodires and chelydrids in having the pectineal processes neither broadly divergent nor parallel.

In most testudinids, including *Platysternon*, the medial surfaces of the ischium and pubis are approximated, usually with a diamond-shaped foramen between the two bones (Fig. 20). The pubis of living chelydrids (and

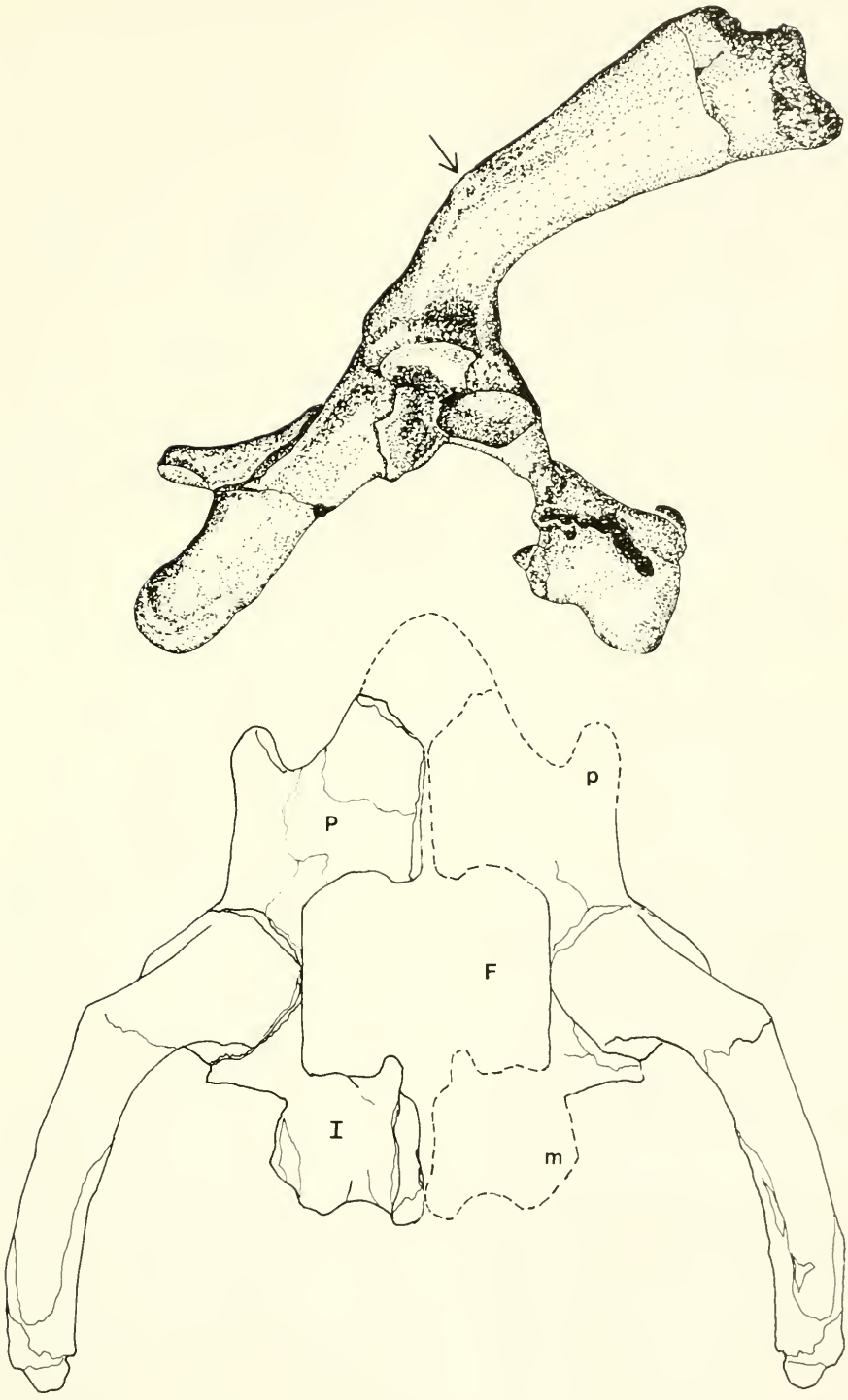

Fig. 19. Above—Left half of pelvis in lateral view. Note thecal process at arrow. Below—Partial restoration of pelvic girdle in dorsal view. Abbreviations as in Figure 20. Natural size.

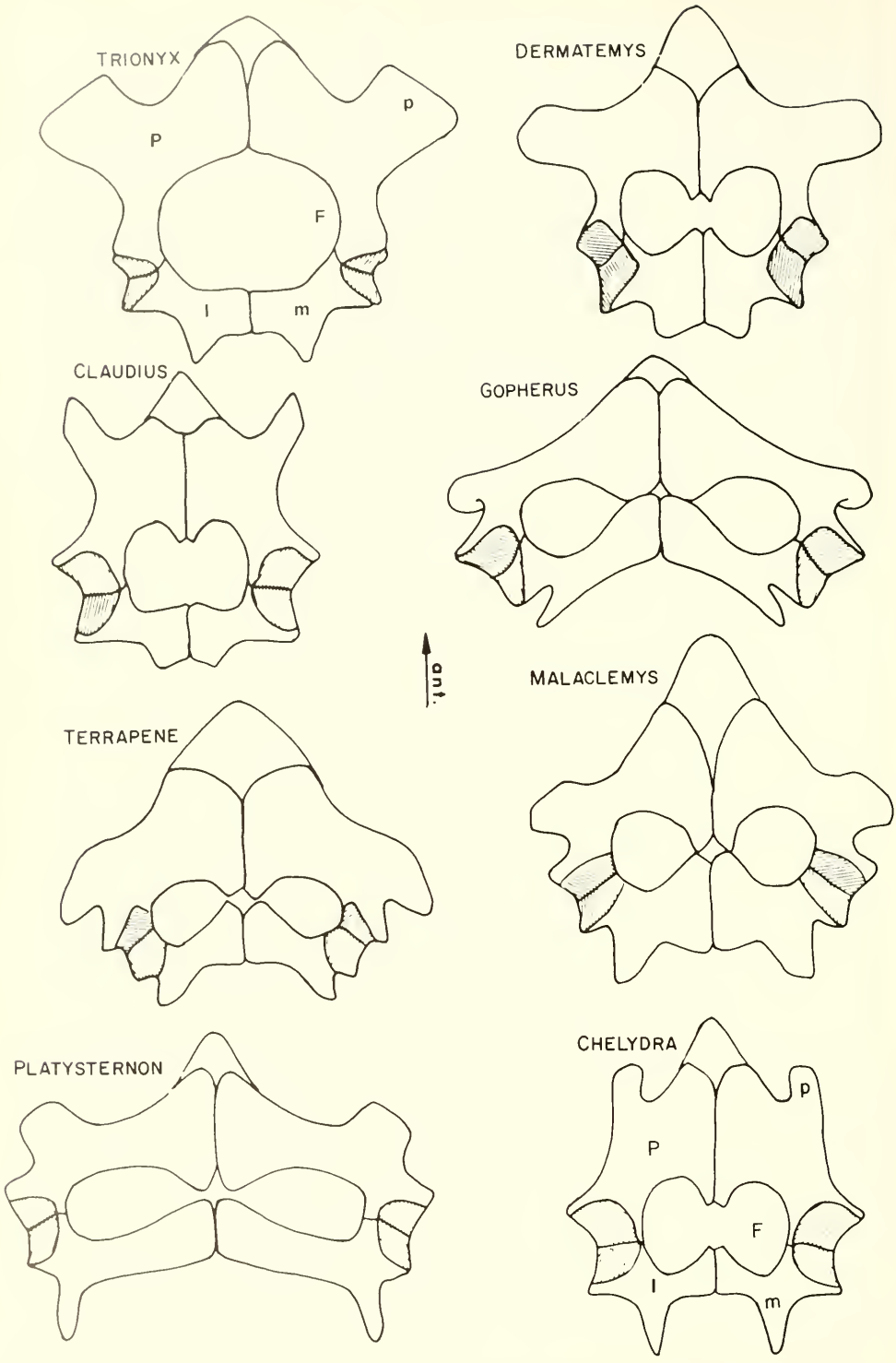

FIG. 20. Pelvic girdles of some cryptodiran turtles in dorsal view, after Zug (1971). Abbreviations: P- pubis, p- pectineal process of pubis, F- puboischiadic foramen, l- ischium, m- metischial process.

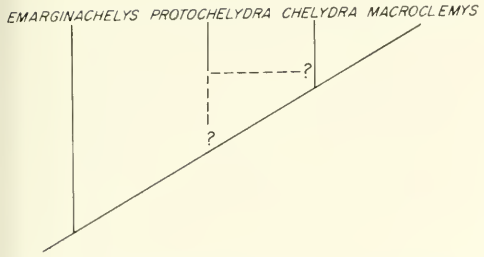

Fig. 21. Alternate hypotheses of the relationships of chelydrid turtles.

Emarginachelys) is relatively widely separated from the ischium, although the cartilage connecting them may calcify late in life. There is no diamond-shaped foramen in living chelydrids or *Emarginachelys*. In *Emarginachelys* there is a ventrally-directed, metischial process not present in *Chelydra* or *Macroclemys*.

PHYLOGENY AND CLASSIFICATION OF CHELYDRID TURTLES

The four genera of chelydrid turtles recognized here (*Emarginachelys, Protochelydra, Chelydra,* and *Macroclemys*) are hypothesized to be a monophyletic group sharing the following derived characters: 1) a cruciform plastron with reduced entoplastron, 2) a long costiform process on the nuchal bone, 3) ligamentous attachment of the plastron to the carapace, 4) an elongate jugal bone, and 5) the pectineal processes of the pubis not broadly divergent. The separation of the abdominal scutes may also be a synapomorphous character, but the impressions of these scutes are not known for *Emarginachelys*. Characters (1) and (3) are also found in toxochelyids and *Claudius,* and character (2) in kinosternids. This distribution is assumed to be the result of convergence since the sister groups of kinosternids and toxochelyids have the primitive condition of these characters.

Protochelydra, Chelydra, and *Macroclemys* are hypothesized to share a common ancestor not shared by *Emarginachelys,* since they share peripheral fontanelles, a closed quadrate, serrated carapacial margin, frontals not bordering the orbits, constriction of the otic bridge, less emarginate skull roof, and formation of a bony "beak" by the premaxillary bone. Parallel pectineal processes may also be synapomorphous at this level. Gaffney (1975b) proposes a unique common ancestor for *Macroclemys* and *Chelydra*. This hypothesis is supported by the presence of plastral fontanelles, reduced xiphiplastra, and a less emarginate temporal region in these genera. An alternate hypothesis is that *Protochelydra* and *Chelydra* share a unique, common ancestry. This hypothesis is supported by the great lateral emargination of the cheek region and the extension of the depression for the pterygoideus musculature anterior to the region of the processus pterygoideus externus. I accept Gaffney's more parsimonious hypothesis and this phylogeny is reflected by the classification which follows.

Gaffney (1975b) placed the Asiatic genus *Platysternon* in the Chelydridae, on the basis of a presumed sister-group relationship to *Macroclemys*. Study of additional specimens of the Miocene *Macroclemys schmidti* indicate that some of the characters assumed by Gaffney to be synapomorphies actually represent convergences (Whetstone, 1978). Also, *Platysternon* lacks the cruciform plastron, narrow epiplastra, "T" shaped entoplastron, serrated carapacial margin, a long costiform process on the nuchal bone, separated abdominal scutes, and parallel pectineal processes of the pubis which are found in *Chelydra* and *Macroclemys*. If *Platysternon* shares a common ancestor with *Macroclemys* not shared by *Chelydra,* these lost characters must be interpreted as evolutionary reversals. *Platysternon* shares at least one presumed synapomorphy with testudinids, as discussed above, and an additional synapomorphy with emydines alone.

A CLASSIFICATION OF CHELYRID TURTLES

Family Chelydridae Swainson, 1839
  Plesion Emarginachelys New Name
  Subfamily Chelydrinae Swainson, 1839
    Genus *Protochelydra* Erickson, 1973
    Genus *Macroclemys* Gray, 1855
    Genus *Chelydra* Schweigger, 1812

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THE UNIVERSITY OF KANSAS
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THE EFFECT OF SLOPE-ASPECT ON THE COMPOSITION AND DENSITY OF AN OAK-HICKORY FOREST IN EASTERN KANSAS

By

Rodney Birdsell and J. L. Hamrick

Vol. 51, No. 18, pp. 565-573 November 28, 1978

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The Effect of Slope-Aspect on the Composition and Density of an Oak-Hickory Forest In Eastern Kansas

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ABSTRACT

Measures of species-diversity, basal area, Importance-Values of individual species and the presence or absence of individual species of trees were compared for north- and south-facing slopes in northeastern Kansas. Basswood (*Tilia americana*) was present only on north-facing slopes. Black walnut (*Juglans nigra*), redbud (*Cercis canadensis*) and bur oak (*Quercus macrocarpa*) were more frequent on north-facing than on south-facing slopes. Red oak (*Quercus rubra*), white ash (*Fraxinus americana*), red elm (*Ulmus rubra*), black oak (*Quercus velutina*), shagbark hickory (*Carya ovata*) and hackberry (*Celtis occidentalis*) were more often present on south-facing slopes. The chestnut oak (*Quercus muhlenbergii*) was found equally distributed on north-facing and south-facing slopes. The more important species present are red oak, black walnut, white ash and shagbark hickory. Previous importance of elms, especially American elm, has been reduced, largely because of the Dutch Elm Disease. North-facing slopes differed from south-facing slopes for all measurements, except for average basal area and overall diversities. The hypothesis is presented that slope-differences are due to the microclimatic variations inherent to the slope-aspect. Biogeographical evidence is given and discussed to support this hypothesis.

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INTRODUCTION

Vegetation varies in response to environmental parameters (Boughley, 1973). At the margins of plant communities these responses may be dramatic, with only slight environmental changes producing marked changes in the dominant vegetation. Such areas occur in northeastern Kansas where sharp ecotones exist between the oak-hickory and the tallgrass-prairie vegetations. Before the arrival of white settlers in the 1850's, these two types of vegetation overlapped in an interdigitating pattern that was determined by various environmental factors (Fitch and McGregor, 1956). Of these factors, availability of moisture is usually considered to be the most important in limiting the extent of oak-hickory forest in eastern Kansas (Weaver et al., 1925). However, changes in environmental parameters such as slope-aspect or edaphic factors may produce subtle but measureable changes in the dominant vegetation.

In this paper, we describe variation in the dominant forest-canopy within the forest-prairie ecotone region of northeastern Kansas and we present the hypothesis that dissimilarities found between the vegetation of north- and south-facing slopes are due to differences in the available moisture inherent to the slope-aspect.

MATERIALS AND METHODS

The study area is a ravine on the John H. Nelson Environmental Study Area (NESA) and is located approximately 15 km. north of Lawrence, Kansas, in southeastern Jefferson County. The longitude and latitude of the area are 90° 12′ W and 34° 03′ N, respectively, and the elevation is approximately 310 meters (1017 feet).

The ravine runs in a westerly direction, forming north- and south-facing slopes with a maximum topographic gradient of 16.8 meters (55 feet). To the north and south of the ravine are areas of grassland, whose management prevents the invasion of woody vegetation. Thus, the only established forest vegetation is either in the ravine or directly adjacent to it.

Three line-transects were established in a north-south direction perpendicular to the direction of the ravine. The transects consisted of trees tagged at breast height with numbered aluminum tags, and served as guidelines for the location of the sample plots. The lengths of the transects, the width of the forest vegetation, are, from east to west, approximately 110 meters, 140 meters, and 250 meters.

Since the transects varied in length, differing numbers of sample plots were systematically placed along each transect. On the eastern transect two 10 x 10 m plots were established, one on the north-facing slope and one on the south-facing slope. The central transect contained a similarly placed pair of plots, plus a third plot located on top of a limestone-outcrop adjacent to the south-facing slope. The western transect consisted of two south-facing and two north-facing plots. Of these four plots, two were located on limestone-outcrops and two were located on the slope below. Thus, a total of nine plots were established, four on the north-facing slope, four on the south-facing slope, and one on a flat area adjacent to the south-facing slope. Within each plot, each tree larger than three inches in diameter at breast height (DBH) was identified to species, was numbered with an aluminum tag, and its DBH was recorded.

From the DBH data, basal areas were calculated for each plot. The basal area for the surrounding woodland was obtained by the Bitterlich Variable-Radius Technique (Cox, 1967). The two basal area measurements were compared to determine if the woodland density for the

plot was representative of the area in which it was located. For each species, the relative density, relative frequency, relative dominance, and Importance-Value were calculated for each plot and for the north- and south-facing slopes.

The Shannon-Weiner Index of Species-Diversity was utilized as a measure of species-diversity. The index is given by $H' = \sum_{i=1}^{S} p_i \ln p_i$, where H' is the index of species diversity for a group of S species, p_i is the relative abundance of ith species, and $\ln p_i$ is the natural logarithm of p_i. Species-diversity for each plot was calculated, and north- and south-facing slopes were compared. In addition to species-diversity, species-abundance (J') was calculated by $J' = H'/\ln S$ (Tramer, 1969), where H' is the Shannon-Weiner Index of Species-Diversity and S is the number of species present.

Data were also obtained from two extraneous sources. An analysis of the physical and chemical soil properties for NESA was conducted during the fall of 1975, and aerial photos from 1941 and 1973 were obtained from the Kansas State Geological Survey.

RESULTS

Six of the nine plots were located on soils mapped either as "Steep and Stony" or as "Detlor Complex," the primary difference being steepness of slope, with 20-45% and 8-18% respectively (USDA, 1977); there were no major chemical differences found for any of the plots. Both soil-mapping units were formed over colluvial material from the limestone-outcrops. The one plot on top of the limestone-outcrop was in the Oska soil series. Except for the two plots located directly on the limestone-outcrops, the eight plots analyzed in association with slope-aspect can be assumed to contain no significant variation in soil quality.

Table 1 ranks all species according to their overall Importance-Values. The more important species were red oak (*Quercus rubra*), black walnut (*Juglans nigra*), white ash (*Fraxinus americana*) and shagbark hickory (*Carya ovata*). The sum of the Importance-Values for these four species was 201.6 (of a possible total of 300). Of these four species, three showed a marked preference for one or the other slope-aspect. The lone exception was red oak, which had only a slightly higher Importance-Value on the south-facing slope. Black walnut had a definite perference for the north-facing slope, while white ash and shagbark hickory favored the south-facing slopes. Marked slope preferences were also shown by species with intermediate or low Importance-Values. The most remarkable of these was basswood (*Tilia americana*) which had an Importance-Value of 46.8 on the north-facing slope, but did not appear on the south-facing slope. Bur Oak (*Q. macrocarpa*) and redbud (*Cercis canadensis*) also had higher Importance-Values on the north-facing slope. Red elm (*Ulmus rubra*), black oak (*Q. velutina*), and hackberry (*Celtis occidentalis*) preferred the south-facing slopes. Only chestnut oak (*Q. muhlenbergii*) failed to demonstrate a slope-preference. Thus, although the coefficient of community of the two slopes was relatively high (0.658 as compared to an expected value of 0.850; Cox, 1972), there is a marked difference in species composition between the two slopes.

Both numbers of individuals and the total basal area were similar in the majority of plots (Table 2). Two plots (1 and 4) were similar to the other plots in terms of total basal area, but, as a result of having few individuals, the average basal area per individual was relatively high. The two plots on the limestone-outcrop (6 and 9) contained numbers of

individuals roughly equal to the other plots, but since each individual tree was relatively large, the total basal area was also large. The total basal area measurements obtained by the Bitterlich technique were similar to those obtained by actual individual measurements except for the two plots on limestone-outcrops. Both of these plots yielded Bitterlich basal area estimates of roughly half that actually present, primarily due to the narrowness of the vegetation directly affected by the outcrops.

Generally, individuals on the north-facing slope were larger than those on the south-facing slope. The ratio between the respective mean basal areas compares favorably with that found in New Jersey by Cantlon in a study on Cushetunk Mountain (Kormondy, 1969). Individuals on the north-facing slope of Cushetunk Mountain averaged 1.8 times greater in basal area than those on the south-facing slope. Individuals on the north-facing slope in the NESA ravine averaged 1.4 times greater in size than those on the south-facing slope.

In contrast to the basal-area differences, the age of the stand appears to be approximately equal for all plots except those on the limestone-outcrops. Aerial photographs from 1941 show little or no forest vegetation within the study area, with the exception of the rock outcrops. The age of the forest can thus be taken to be somewhat less than 40 years.

Both species-richness and species-abundance were measured by the Shannon-Weiner Index of Species-Diversity. Species-richness, or the number of species present, ranged from three species per plot to six species per plot. Although neither slope contained substantially greater numbers of species per plot, certain species (especially basswood) did demonstrate a slope preference. The species-abundance factor (I') was slightly higher for the north-facing plots than for the corresponding south-facing plots, indicating that north-facing plots possess a more nearly equal distribution of species.

DISCUSSION

The most dramatic effect of slope-aspect is the variation in individual species' Importance-Values (Table 1). Of the eleven species found, the three demonstrating the more widely variable Importance-Values were basswood, white ash, and black walnut. Basswood appeared only on the northfacing slope, yet possessed the third Importance-Value for that slope, being surpassed only by black walnut and red oak. Furthermore, only basswood demonstrated a strong slope-preference and a strong preference for the number of plots on which it appeared.

Of the three species demonstrating a major slope-preference, basswood has the most limited geographical distribution (Little, 1971). Within the forest-prairie ecotonal region of eastern Kansas, the major environmental parameter limiting the western distribution of basswood is precipitation. It therefore follows that micro-climatic heterogeneity in moisture-availability should be reflected by micro-distributional patterns of basswood more than for species with greater ecological amplitudes.

This result is consistent with several studies which reveal that north-facing slopes remain cooler and contain more moisture than corresponding south-facing slopes. In one such study conducted in Michigan during the 1957 growing season (Cooper, 1960), the air-temperature fifty cm. above the ground averaged nearly 5°F higher on the south-facing slope than on the north-facing slope. In addition, soil-temperatures at depths of 2 and 20 cm. produced similar differences, and the percent of moisture (by weight) of the soil at a depth of 2 cm. was as much as

12.7% higher for the north-facing slope. Thus, the north-facing slope was better able to supply moisture to the vegetation during periods of stress by drought.

A similar study by Cantlon on Cushetunk Mountain in New Jersey lists temperatures from 3.5-6.0°F higher for the south-facing slope than for the north-facing slope (Kormondy, 1969). As a result of the higher temperatures, the south-facing slope has a larger vapor-pressure deficit, and more evaporation. Even greater extremes in the microclimate have been shown to exist between northeast- and southwest-facing slopes (Benson et al., 1967). Therefore, in eastern Kansas where water availability is one of the more important environmental parameters influencing vegetational composition, it is not surprising to find mesophytic species restricted to north and east-facing slopes. Moreover, since this forest is only approximately 40 years old, we can assume that it has not yet reached a stable climax. As the forest continues to mature, we might expect to observe a greater heterogeneity in vegetational composition between the slopes (Odum, 1969). Furthermore, the more mesic north-facing slope might be expected to approach a stable climax more rapidly.

Further evidence for the more favorable micro-climate of the north-facing slope is provided by the differences in basal area observed between the two slopes. Since aerial photography indicates that the majority of the existing forest vegetation dates from the late 1930's and early 1940's, we can assume that these differences are due to faster growth rates on the north-facing slope. However, without a homogeneous species-composition and age-structure between slopes, no definite conclusions can be drawn in regards to absolute growth-rates (Geyer and Naughton, 1970). The fact does remain, however, that the north-facing slope presently supports a larger basal area per individual.

Micro-climatic differences due to slope-aspect may not be the only environmental factors that have influenced the present vegetation of this ravine. Drought, which occurs in the Great Plains on approximately 20-year cycles, has had a large effect on the vegetation of eastern Kansas and may provide an additional explanation for the restriction of such species as basswood to north-facing slopes. During periods of severe drought, such as that of the 1930's, such species may have been unable to survive on the drier, south-facing slopes (Albertson and Weaver, 1945).

Biological factors such as disease may also have had major effects on the composition of the NESA forest. Dutch Elm Disease was first diagnosed in Jefferson County in 1961 and it had been reported in neighboring counties as much as three years earlier (Kainski et al., 1964). In the early 1950's, at the University of Kansas Natural History Reservation (located approximately 3 km south of NESA), ⅓ to ½ of the trees greater than six inches DBH were elms (Fitch and McGregor, 1956). In contrast, of the 74 trees included in this study only five were elms.

The decline of the American elms was relatively rapid, following the introduction of Dutch Elm Disease to Kansas. Before the advent of the disease, Fitch and McGregor (1956) stated that American elm (*Ulmus americana*) was much more prevalent as a dominant tree than red elm (*Ulmus rubra*), with few red elms being over 12 inches (30.5 cm) DBH, although "the saplings of this species constitute a prominent part of the understory." A comparison between two studies (Wells and Morley, 1964 and unpublished class data, 1975) of Baldwin Woods, 30 km. south of NESA indicates that by the mid-1960's the population of elms had reached a relatively stable equi-

librium (Table 3). It should be noted that in both studies, the disease resistant red elm is more important, a reversal of the previous observations of Fitch and McGregor (1956). From the above, one can conclude that the elms, particularly the American elm, have been removed as major dominants in the forest canopy within the last 20 years.

Other species may have also been selectively removed from the area by the activities of man. Logging of Jefferson County and nearby Douglas County has been widespread for more than 100 years (Fitch and McGregor, 1956) and there is evidence of logging within the NESA area. In addition to the observation of several large, sawed stumps, several individuals of red oak and black walnut have multiple trunks emitting from a common root system. As red oak and black walnut are among the species most heavily used by the lumber-industry in Kansas (Deneke and Funsch, 1970), it is likely that the multiple trunks sprouted after logging. Age measurements of one such multiple trunk-system revealed that the ages of the separate trunks were within a range of five years. Other tree-cutting activities, such as the rural practice of heating and cooking with wood, also accounted for a share of the woodland disturbance until about 1940.

Although the sampling methods were not identical, one can compare the results of this study with two others done within a nearby forested area. Both Wells and Morley's (1964) study and unpublished data from a University of Kansas class (1975) involved Baldwin Woods, an unglaciated area 30 km. south of NESA. The major finding of the 1975 study was that the topographic position on the slope was as important as slope-aspect in determining the composition of the canopy. However, the topographic gradient of Baldwin Woods is much greater than that of the NESA ravine (circa 100 meters versus 16 meters). While in both instances the slope-aspect largely determines canopy composition, conclusions relating to the much larger topographic gradient of Baldwin Woods are not directly applicable to the site at NESA.

A higher species-diversity was also found in the Baldwin Woods studies. While some of this increase could be explained by the greater topographic diversity of Baldwin Woods, the major factor appears to be the greater edaphic diversity there. Baldwin Woods is unglaciated and has a variety of parent materials while the soils of NESA were formed primarily of colluvium from the limestone-outcrops, with both loess and glacial till being influential. Other than the actual limestone-ledges (Plots 6 and 9), the soils in the study area have formed from virtually identical parent materials.

The overall diversity within the forest canopy can also be shown to be dependent upon a set of limiting factors. In both the NESA study and Tramer's (1969) study of 267 bird populations, diversity was dependent upon the number of species (species-richness). For the NESA plots, the population diversity (H') correlated at significant levels ($r = 0.975$ and 0.939) with ln S, the natural logarithm of species-richness. This relationship contrasts with that of phytoplankton in which the species-richness remains stable, and species-diversity is linked to the relative abundance of species (Sager and Hasler, 1969). Certain phytoplankton species are "opportunistic," and may experience dramatic fluctuations in population size in response to changes in availability of resources. Thus, although the number of species in a given area may remain approximately the same over a period of time, estimates of species-diversity will decrease due to changes in relative abundance.

Conversely, Tramer (1969) notes that birds are "equilibrating," since the environmental factors of a given habitat determine the number of species which can exist in that habitat. As species-diversity for the NESA tree-canopy was comparable to Tramer's bird populations in terms of dependence on species-richness, the diversity of the forest-canopy may also be a result of environmental parameters which regulate the number of species that can exist in a given area.

In summary, extensive pressures due to logging, fire, farming practices, Dutch Elm Disease, and periodic droughts have contributed to the present condition of this forest. However, micro-climatic differences in moisture availability are also of great importance. There is an increase in temperature, evapotranspiration, and water stress on the south-facing slope, resulting in a more favorable micro-climate for forest vegetation on the north-facing slope. The more favorable micro-climate is shown by a shift in species composition within the forest-canopy and by larger basal areas per individual for the north-facing slope.

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TABLE 1.

A listing of the eleven tree species appearing in the NESA study plots in order of decreasing Importance-Values. The effect of slope-aspect on numbers, frequency, density, dominance and importance is also given.

	# Individuals	Relative Frequency	Relative Density	Relative Dominance	Importance Value	Average Importance Value
Red Oak						
North-facing	4	17.6	13.3	25.0	55.9	59.6
South-facing	6	17.6	15.4	30.3	63.3	
Black Walnut						
North-facing	6	17.6	20.0	33.0	70.6	53.2
South-facing	3	11.8	7.7	16.2	35.7	
White Ash						
North-facing	3	11.8	10.0	1.8	23.6	44.3
South-facing	11	17.6	28.2	19.2	65.0	
Shagbark Hickory						
North-facing	3	11.8	10.0	3.6	25.6	34.5
South-facing	9	11.8	23.1	8.5	43.4	
Red Elm						
North-facing	1	5.9	3.3	10.0	19.2	25.1
South-facing	4	11.8	12.8	6.3	30.9	
Bur Oak						
North-facing	4	5.9	13.3	11.2	30.4	25.0
South-facing	1	5.9	2.6	11.1	19.6	
Basswood						
North-facing	6	17.6	20.0	9.2	46.8	23.4
South-facing	0	0.0	0.0	0.0	0.0	
Chestnut Oak						
North-facing	2	5.9	6.7	5.2	17.8	19.4
South-facing	2	11.8	5.1	4.2	21.1	
Black Oak						
North-facing	0	0.0	0.0	0.0	0.0	6.0
South-facing	2	5.9	2.6	3.4	11.9	
Red Bud						
North-facing	1	5.9	3.3	0.9	10.1	5.0
South-facing	0	0.0	0.0	0.0	0.0	
Hackberry						
North-facing	0	0.0	0.0	0.0	0.0	4.6
South-facing	1	5.9	2.6	0.8	9.3	

TABLE 2.
Basal area for each sample plot and average basal area per individual.

PLOT	ASPECT OF SLOPE	NUMBER OF INDIVIDUALS PER PLOT	BASAL AREA PER PLOT (SQ. IN/100M^2)	BITTERLICH BASAL AREA MEASUREMENT (SQ. IN/100M^2)	BASAL AREA PER TREE (SQ. IN.) (S.D.)
1	North	4	203.29	263.41	50.82 ± 39.12
2	South	8	221.62	312.19	27.70 ± 11.55
3	North	8	216.94	282.92	27.12 ± 4.94
5	South	12	258.58	243.90	21.55 ± 4.13
7	North	10	323.01	292.88	32.20 ± 6.69
8	South	10	257.35	253.66	25.72 ± 4.40
6*	North	8	866.58	390.24	108.32 ± 34.36
9*	South	9	746.64	409.75	82.96 ± 26.14
4**	Neither	5	284.70	243.90	56.94 ± 23.64
All North Mean		7.50	402.46	307.36	53.70
(Plots 1, 3, 6 and 7)		(±2.52)	(±314.01)	(±56.39)	(±65.38)
All South Mean		9.75	371.05	304.88	38.08
(Plots 2, 5, 8 and 9)		(±3.37)	(±250.98)	(±76.14)	(±47.15)
Overall Means		8.24	375.41	299.21	45.68
(Plots 1-9)		(±2.49)	(±249.00)	(±61.70)	(±55.71)

* Plots 6 and 9 are located on rocky outcrops.
** Plot 4 is on a level area adjacent to a south-facing slope.

TABLE 3.
Comparison of the importance of elm species in three studies located in eastern Kansas. The 1956 study was before the introduction of Dutch Elm Disease.

		1956[3] Nat. Hist. Res.	1964[4] Baldwin Woods	1975[5] Baldwin Woods
Red Elm	I.V.[1]	*	18.3	22.0
(*Ulmus rubra*)	Freq.[2]	*	8.7	6.4
American Elm	I.V.[1]	*	2.5	3.0
(*Ulmus americana*)	Freq.[2]	*	0.8	1.1
Ulmus spp.	I.V.[1]	*	*	*
(9 total)	Freq.[2]	25.8[6] to 57.9[7]	9.5	7.5

[1] Importance Value; [2] Frequency (in percent); [3] Fitch and McGregor, 1956; [4] Wells and Morley, 1964; [5] Unpublished class data, University of Kansas; [6] For trees greater than one foot DBH on a West Slope; [7] For trees six inches to one foot DBH on a South slope; * Not listed.

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POLLEN MANIPULATION AND RELATED ACTIVITIES AND STRUCTURES IN BEES OF THE FAMILY APIDAE

By
Charles D. Michener, Mark L. Winston,
and
Rudolf Jander

Vol. 51, No. 19, pp. 575-601 December 8, 1978

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Pollen Manipulation and Related Activities and Structures in Bees of the Family Apidae[1]

Charles D. Michener[2, 3, 4], Mark L. Winston[2], and Rudolf Jander[2, 3]

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ABSTRACT

Pollen manipulation is described for all major groups of Apidae, and for comparative purposes, other bees are also considered. In *prototypic* pollen collecting, pollen is removed from the front legs and head, and carried in the crop. In *eutypic* pollen collecting, it is removed from the front and mid legs as well as surfaces of the head and thorax and transferred by the middle legs to the scopa on the hind legs. Different *derived* or *metatypic* types of pollen manipulation supplement the eutypic behavior and provide for transfer of pollen to the abdominal scopa in the Megachilidae and from the abdomen to the hind tibiae in the Apidae.

In Apidae the brushy scopa of many other bees is modified into a corbicular scopa, which with the hind tibial surface forms the corbicula. Corbicular filling (= pollen packing) can be

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achieved with little or no modification of eutypical behavior; for Apidae this is called Type I pollen packing, in which pollen is put directly into the corbiculae by the middle legs. Nesting materials are packed and transported in the same way. On the other hand, the corbicula is usually loaded with pollen from its distal end. This is Type II pollen packing. It may be either (a) ipsilateral, a modified eutypic pattern in which pollen is placed on the outside of the tibiotarsal joint by the middle leg of the same side, and thence pushed basad into the corbicula, or (b) contralateral, a derived pattern in which pollen transferred by the middle legs to the inner surfaces of the hind basitarsi or swept from the abdomen by those basitarsi, is transferred to the corbicula of the opposite tibia.

In pollen-manipulating movements and structures, certain Meliponinae appear to be the most primitive apids, apparently lacking Type II pollen-packing behavior as well as structures necessary for it. For other Meliponinae, ipsilateral Type II pollen packing is most important, although some have contralateral Type II behavior as part of their repertoire. The small hind basitarsus without an auricle suggests that contralateral Type II packing is of little importance in most Meliponinae, although an auricular area can function like the auricle to push pollen basad into the corbicula. Euglossini are inadequately studied, but probably exhibit ipsilateral Type II behavior. Bombini and Apinae are similar to one another in pollen-handling structure and behavior and for both, contralateral Type II pollen packing is a principal method.

Modifications of usual pollen-manipulating movements are seen in scent manipulation by male euglossine bees and in pollen-gleaning activity by certain Meliponinae *(Scaura)*.

Most of the pollen-manipulation movements are either the same as self-grooming movements or are opposites of them so that, for example, a structure that is stroked distally for cleaning may be stroked basally to load it with pollen, the cleaning movement proper serving later for unloading. Presumably such loading movements are derived from similar cleaning movements. Only the hind basitarsal movements that push pollen basad into the corbicula lack counterparts in cleaning or other known behavior.

INTRODUCTION

The purpose of this paper is to describe movements whereby pollen and other materials are collected and placed for transport in the apid "pollen baskets" or corbiculae, the derivation of these movements from self-grooming behavior, and the meaning of these movements and related structures for apid evolution. Morphological and behavioral features for collecting and transporting materials play a crucial role in the evolution and adaptive radiation of the bees (superfamily Apoidea). These features are therefore important both for bee taxonomy and for evaluating homologies and convergence (Michener, 1944, 1974; Jander, 1976; Winston and Michener, 1977). While the adaptations for transport of nonliquid materials in most families of bees relate primarily to pollen, in the Apidae they are also associated with the transport of materials used in nest construction.

The family Apidae is divided into four distinct groups, the subfamily Meliponinae (the sister group to all the rest according to Winston and Michener, 1977), the tribes Euglossini and Bombini (currently united in the subfamily Bombinae), and the subfamily Apinae. In the past, pollen-collecting behavior has been well described only for the Apinae; progressively less was known about this behavior in the Bombini, Meliponinae and Euglossini (Maurizio, 1968).

While some female bees (Euryglossinae, Hylaeinae) transport pollen to the nest exclusively in the crop, most carry at least part of their pollen harvest with the help of hairs which are located differently in the various taxonomic groups. Such hairs form the scopa, a term applied to

pollen-carrying hairs whether they are on the outer sides of the hind tibiae and basitarsi, the under sides of the basal segments of the hind legs, the sides of the propodeum, or the under surface of the abdomen (Braue, 1913; Michener, 1944). In the Apidae and the family most similar to it, the Anthophoridae, the scopa is largely restricted to the outer side of the hind tibia, a restriction unusual in other families of bees (but see the Panurginae in the Andrenidae). While the scopa is brushy in the Anthophoridae, it is reduced in the Apidae to a corbicular scopa or fringe surrounding a smooth and often concave surface on the outer side of the tibia; the fringe and surface together constitute the corbicula or pollen basket. The manner in which the corbicula is filled is the major topic of this paper; the process is sometimes called pollen packing.

In most bees which carry pollen on the scopa of the hind legs, unmoistened pollen is swept off of anthers or off the hairs of the bee's head by the front basitarsi, then transferred to the middle legs which also typically sweep pollen off the thorax. The middle legs then transfer their pollen to the scopa. These movements have been seen in halictids, andrenids, and in anthophorids as different as *Ceratina, Xylocopa, Melissodes,* and *Svastra* (R.J., personal observations). In many cases (e.g., for halictids, Michener and Wille, 1961; Batra, 1966; Roberts, 1969; for *Andrena* spp., Michener, unpublished) these movements occur while the bee is on the flower, supported by its legs, and only one leg moves at a time; the legs of a pair are not synchronized. (The repertoire of these bees may also include movements, perhaps synchronous, performed in flight; leg movements during flight have not been investigated.)

The movements for pollen handling and transport appear to be combinations and modifications of apoid self-grooming movements (Jander, 1976, and in preparation). The transfer of dirt (in grooming) is consistently from anterior to more posterior legs and it is commonly discarded from the hind legs. The same is true in the case of pollen transfer, but cleaning of the posterior legs is delayed until the bee is in its nest where it removes the pollen to be used for larval or adult food.

We have been much impressed by the well known fact that bees of the same species, no doubt often the same individuals, exhibit different pollen-collecting behavior on different kinds of flowers. The repertoire of each species is probably extensive. Therefore, conclusions about the evolution of the behavioral patterns or the phylogeny of the bees as shown by such patterns are presented with some hesitation. For example, it is always possible that a behavioral pattern thought to be restricted to a derived group of bees will be found as an uncommon pattern, or perhaps commonly with pollen of a particular consistency, in a primitive group. Nonetheless, we have interpreted our findings in evolutionary terms, we believe with justification, even though more observations will doubtless extend the known taxonomic range of some behaviors.

MATERIALS

Observations of pollen packing and related transport behavior have been made by us and by prior authors on the species listed below. Each species name is followed by the number of critical observations of pollen packing where known (in parentheses), location, and the observers (initials for the authors of the present paper) or literature references.

Meliponinae:

Trigona (Trigonisca) buysoni (6); Rio Anchicayá, Prov. del Valle, Colombia, collecting pollen from *Hedychium coronarium* (C.D.M.).

Trigona (Paratrigona) impunctata (10); 7.5 km southwest of Kourou, French Guiana, collecting pollen from a large-flowered *Cassia* (C.D.M., M.L.W.); 6 km southwest of Kourou, French Guiana, collecting

pollen from *Stylosanthes* (C.D.M.); 12 km southwest of Kourou, French Guiana, collecting pollen from melastomaceous shrub (C.D.M.).

Trigona (Paratrigona) subnuda; State of Paraná, Brazil, collecting pollen from *Tibouchina* spp. (Laroca, 1970).

Trigona (Paratrigona) sp.; Pichinde, Prov. del Valle, Colombia, on flowers of *Baccharis* (?) (C.D.M.).

Trigona (Scaptotrigona) pectoralis; Pichinde, Prov. del Valle, Colombia, on flowers of *Baccharis* (?) (C.D.M.).

Trigona (Scaptogrigona) postica; Rio Claro, São Paulo, Brazil, collecting cerumen from old *Trigona* nest (Sakagami and Camargo, 1964).

Trigona (Cephalotrigona) capitata (10); 6 km southwest of Kourou, French Guiana, collecting pollen from *Stylosanthes* (C.D.M.).

Trigona (Tetragona) clavipes (8); Kourou, French Guiana, collecting pollen from white *Ipomoea* (C.D.M., M.L.W.).

Trigona (Tetragona) fimbriata; near Kuala Lumpur, Malaysia, 10 specimens with pollen loads, no behavioral observations (C.D.M.).

Trigona (Tetragona) jaty; Costa Rican colony introduced to laboratory at Lawrence, Kansas, by E. M. Barrows, collecting pollen from *Prunus* (R.J.).

Trigona (Tetragona) thoracica and *itama;* Kepong near Kuala Lumpur, Malaysia, collecting pollen from *Cassia spectabilis* (R.J.).

Trigona (Trigona) amalthea (= trinidadensis) (10); highway summit west of Cali, Prov. del Valle, Colombia, collecting pollen from *Cucurbita pepo* (C.D.M., M. D. Breed, W. J. Bell).

Trigona (Trigona) fulviventris fulviventris, fuscipennis, and *silvestriana;* Prov. de Guanacaste, Costa Rica, collecting pollen from *Cassia biflora* (Wille, 1963).

Trigona (Trigona) nigerrima (many); Rio Anchicayá, Prov. del Valle, Colombia, collecting pollen from *Hedychium coronarium* (C.D.M., M. D. Breed; cinematography by M. D. Breed).

Trigona (Trigona) pallida (many); Kourou, French Guiana, collecting pollen from white *Ipomoea* (C.D.M., M.L.W.); 7.5 km southwest of Kourou, collecting pollen from a large-flowered *Cassia* (C.D.M., M.L.W.).

Trigona (Trigona) spinipes and *fulviventris guianae;* State of Paraná, Brazil, collecting pollen from *Tibouchina* spp. (Laroca, 1970).

Trigona (Trigona) fulviventris guianae; 12 km southwest of Kourou, French Guiana, collecting pollen from melastomaceous shrub (C.D.M.).

Trigona (Scaura) latitarsis; State of Maranhão, Brazil, collecting pollen from *Piper* and *Amaranthus* (Laroca and Lauer, 1973).

Trigona (Scaura) longula (10); 7.5 km southwest of Kourou, French Guiana, collecting pollen from a large flowered *Cassia* (C.D.M., M.L.W.).

Melipona fasciata and *favosa;* French Guiana, fresh specimens with pollen loads of various sizes (M.L.W.). Loading behavior not observed because of rapid flight.

Melpiona fasciata; Osa Peninsula, Costa Rica, collecting mud (R.J.).

Melipona pseudocentris; 12 km southwest of Kourou, French Guiana, collecting pollen from melastomaceous shrub (C.D.M.).

EUGLOSSINI:

Euglossa cordata group and *E. ignita* (20); 49 km south of Cayenne and 19 km southwest of Kourou, French Guiana, collecting pollen from *Sabicea* near *cinerea* (C.D.M., M.L.W., G. Otis).

Euglossa cordata group (2); Kourou, French Guiana, collecting cerumen from an old *Trigona* nest (C.D.M.).

Euglossa cordata group (10); vicinity of Kourou, French Guiana, males collecting cineole and other scents (C.D.M.).

Euglossa championi (many); Rio Anchicayá, Prov. del Valle, Colombia, males collecting cineole and other scents (C.D.M., M. D. Breed; cinematography by M. D. Breed).

Eulaema cingulata (1) and *Euplusia auripes* (2); vicinity of Kourou, French Guiana, males collecting cineole and other scents (C.D.M.).

BOMBINI:

Bombus spp.; Europe, pollen collecting (Hoffer, 1882; Sladen, 1911, 1912a; Buttel-Reepen, 1915).

Bombus cayennensis; 45 km southwest of Cayenne, French Guiana; fresh specimens with pollen loads (C.D.M.).

Bombus pennsylvanicus (= americanorum); Baldwin, Kansas, pollen collecting on *Cassia chamaecrista* (observations and cinematography by R.J.).

APINAE:

Apis mellifera; Europe and North America, pollen collecting (Sladen, 1912b; Parker, 1926; Beling, 1931; Ribbands, 1953; Snodgrass, 1956; Legge and Bole, 1975); Lawrence, Kansas, pollen collecting on *Cytisus scoparius* (R.J.); Europe, Brazil, resin (propolis) collecting (Sladen, 1911, 1912b; Rösch, 1927; Meyer, 1953, 1954, 1956; Sakagami and Camargo, 1964); Lawrence, Kansas, resin (propolis) collecting (observations and cinematography by R.J.).

METHODS

Behavior while a bee is on a flower is usually easily observed, but much of the pollen manipulation in the Apidae occurs in flight. Certain individuals, especially of the genus *Trigona,* hover briefly and rather quietly close to the flowers, and can be watched against the background of the flowers when desired. They then often return to the same flower for more pollen, and repeat the hovering. Such individuals are the principal sources of our new data on leg movements. Considerable detail was visible and the behavior pattern was pieced together from observations of many different hovering individuals, mostly of *Trigona pallida* and *nigerrima,* from all possible

angles. C.D.M. and M. D. Breed observed pollen manipulation by *Trigona* as well as leg movements of male euglossine bees in southwestern Colombia; Dr. Breed made moving pictures which were later analyzed by C.D.M., R.J. made moving pictures of resin collecting by *Apis mellifera* and of pollen collecting by *Bombus pennsylvanicus*. The films were analyzed with the invaluable help of a Super 8 Lafayette Analyzer Projector.

Another source of information is pollen on the legs of bees killed while collecting pollen. The anatomical details and the location of pollen accumulation help in determining the packing behavior. These data, collected by C.D.M. and M.L.W. and recorded largely as sketches and notes made at Kourou, French Guiana, usually substantiate the behavioral data.

Various behavioral matters that are not directly related to filling the corbiculae are mentioned in passing. To save space, references in such cases are not usually included, but can be found in Michener (1974).

The terminology used for the movements involved in pollen manipulation is that of Jander (1976). In *rubbing,* two parts move back and forth, one against the other, without losing contact throughout the action. In *scraping,* strokes in one direction involve contact, but the parts are separated for the return strokes. For hairy structures such as many bees have, these terms may not seem ideal; words like brushing or combing are more descriptive. However, they do not indicate the distinction drawn between rubbing and scraping and are avoided except when our observations are not good enough to make that distinction.

Orientational terms for the legs, especially for movements relative to the hind tibia, can be confusing. In the tibia's usual position, upward might be regarded as toward the base. Because it is moveable, that usage is avoided, and we use instead *basad,* toward the base or femoral articulation, and *apicad,* toward the apex. These are simply directional terms; a basad movement can occur near the apex of the tibia. Because the tibia is often extended posteriorly, *upward* is taken to be toward the upper margin, i.e., at right angles to the long axis of the tibia. The same direction relative to the tibia can be called *posterior* if the long axis of the tibia is considered to be vertical.

TRANSPORT OF NESTING MATERIALS

Species of *Melipona* are regularly seen collecting mud and carrying it in the corbiculae, and *Melipona* and *Trigona* both carry cerumen from other nests, as well as gums and resins, in a similar way. Some species of *Trigona* also carry vertebrate fecal material, mud, or chewed plant material in the corbiculae. Bassindale (1955) gives an account of propolis packing by *T. braunsi* and Sakagami and Camargo (1964) illustrate and give an account of the similar packing of cerumen for transport by *T. postica.* The latter authors report that the mandibles cut out particles of cerumen which are manipulated and pressed together to form a lump by the mandibles and forelegs (probably basitarsi, C.D.M.). "When the lump attains an appropriate size, one of the middle legs reaches forward, and using bristles on its underside (basitarsus? C.D.M.), the bee transfers the lump very rapidly to the corbicular surface of the hind leg of the same side, which is synchronously moved a little forward." By repetition of these movements, the accumulation on the corbicula grows. Often the middle leg is extended back, and gently presses the growing ipsilateral (same side) corbicular deposit. One or both of the hind legs may be raised in a peculiar way above the wings; the function of this movement, if any, is unknown.

One of us (R.J.) has observed collecting and transport of mud by *Melipona fasciata.* Biting with the mandibles and scratching with the forelegs, the bee loosens a bit of moist mud, which is then taken up by the mandibles. With a backward motion, one foreleg takes the bit of mud from the mandibles. The ipsilateral middle leg scrapes the piece of mud from the foreleg by clasping the foreleg from the outside. This movement appears identical to the cleaning of the foreleg by the middle leg during a normal cleaning bout (Jander, 1976). The middle leg then passes the mud backward and presses it from the outside into the corbicula. This is usually followed by patting movements of the middle leg on to the mud in the corbicula. Only unilateral (one side at a time) transfer of mud was observed; mud may be passed backward on one side several times

before the bee uses the other side. After both corbiculae have been filled, but before taking flight, the bee takes a larger lump of mud between the mandibles, first holding it with both forelegs and then pressing it to the mandibles.

Euglossa and *Euplusia* carry resin in the corbicula and *Eulaema* carries vertebrate fecal material as well as resin. *Euplusia* sometimes carries small pieces of bark stuck to the resin, if museum specimens with such bark are meaningful. One female of the *Euglossa cordata* group was observed taking cerumen from fragments of an abandoned *Trigona* nest. Few observations were possible, so that details are not available, but the bee clearly detached pieces of cerumen with its mandibles, then hovered and while in the air transferred the cerumen to the corbiculae. The middle legs clearly were seen to synchronously carry pieces back to the ipsilateral hind legs which were brought forward, the middle legs then patting the cerumen into the corbiculae. The bee then alit to obtain more cerumen. The cerumen masses on the corbiculae became large and irregular. Because of behavior in other groups as well as in euglossine males described below, we suspect that euglossines may not always hover to transfer sticky materials to the corbiculae synchronously with both middle legs. Nonflying Meliponinae and Apinae have been seen to transfer sticky materials to the corbiculae asynchronously, with one middle leg at a time.

Bombus constructs its nests using a mixture of wax and pollen. Wax is secreted by the bees. So far as known, pollen is not transported differently for construction than for food; in fact young larvae may eat some of the wax-pollen mixture. Transport of pollen is described below.

Apis mellifera, both in Europe and the Africanized bees in Brazil, collects resin (propolis) or cerumen exactly as described above for *Trigona postica* except that the hind legs are not raised (Sladen, 1912b; Rösch, 1927; Meyer, 1953, 1954, 1956; Sakagami and Camargo, 1964; see IBRA, 1976). One of us (R.J.) made additional observations of such behavior, summarized as follows: The mandibles gnaw the surface of the resin while at the same time the forelegs and occasionally the middle legs scrape and scratch the surface. Loosened pieces are released by the mandibles to both forelegs. In a very quick movement, one foreleg swings backward and the ipsilateral middle leg grasps the foreleg from the outside and scrapes off the propolis. The femorotibial joint of the middle leg is sharply bent in this operation (as when the middle leg cleans the foreleg in grooming, Jander, 1976) and the piece of propolis sticks to the inner posterior side of the mid basitarsus, presumably held by the sharp bristles in that area. Immediately the middle leg swings backward and the piece of propolis is pressed by the mid basitarsus onto the corbicula of the ipsilateral hind leg. Then the middle leg is pulled forward while still in contact with the hind leg; the resultant scraping movement leaves the resin in the corbicula. The pressing and scraping may then be repeated a second time. All these movements were performed while the bees were on the ground.

MANIPULATION OF SCENTS BY MALE EUGLOSSINI

Male euglossine bees collect certain scented substances from orchid flowers and other sources (Vogel, 1966) and can be attracted to scents provided artificially (Dodson et al., 1969). Interestingly, the movements involved are similar to those of pollen collecting by females, although other male bees, so far as known, use similar movements only for self-grooming. Several species were observed; the following observations apply equally to *Euglossa, Euplusia,* and *Eulaema,* and largely support

the detailed accounts and illustrations by Vogel (1966) and Evoy and Jones (1971). (The middle tibia cited by the latter authors appears to have been in reality the middle basitarsus.)

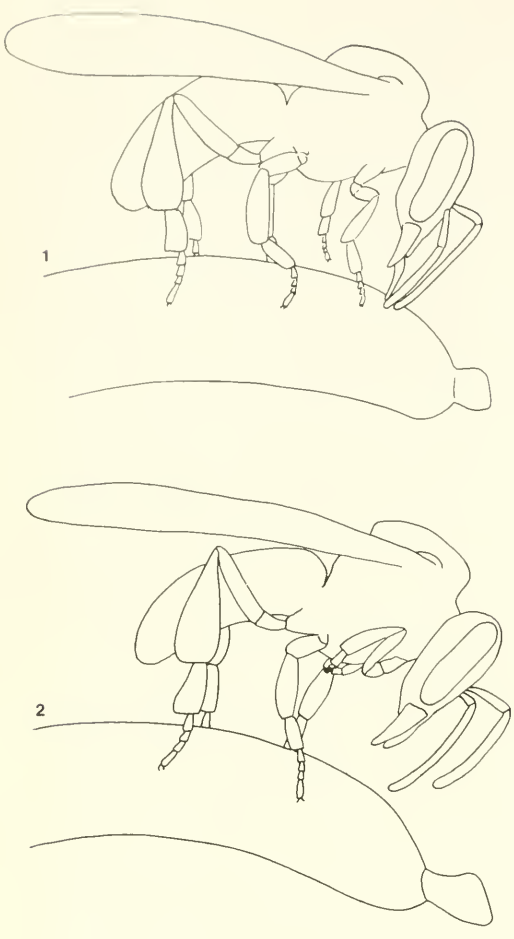
The front tarsi are rubbed on the material containing the attractant; sometimes they also scrape the head, especially the eyes, downward and forward as in grooming movements. The proboscis is not exerted; the tips of the antennae are directed down to or almost to the scent source. After such rubbing, the bee usually hovers and while in the air the middle legs move forward synchronously and apparently scrape the fore tarsi with the under surfaces of the ipsilateral mid basitarsi. The middle leg is probably flexed as in normal cleaning of the foreleg. The middle legs now move back, and at the same time the hind legs are synchronously flexed and rotated forward. Now the under surfaces of the mid basitarsi scrape synchronously upward, i.e., at right angles to the long axes, across the outer surfaces of the enlarged hind tibiae. The two structures are nearly parallel to one another, and only at the end of each stroke may the mid basitarsus contact the hairs of the dorsal metatibial groove. The whole sequence is repeated several times while the bee is hovering, before it alights again at the source of the scent, or departs. The greater part of the contact of the middle tarsus with the hind tibia is with the simple, convex, short-haired, outer, tibial surface and not with the groove which is supposed to absorb the attractant substances.

Rarely, instead of hovering, a bee grasps the edge of a leaf with its mandibles after rubbing an attractant with its front tarsi, and then, hanging by the mandibles, it goes through the leg movements described above. It thus frees the middle and hind legs for the movements usually performed while hovering.

APID POLLEN MANIPULATION

The Forelegs. As in most other bees, the front legs (basitarsi) and the proboscis remove pollen from the anthers of flowers; pollen on the proboscis and the head is subsequently scraped off by the forward and downward movements of the front legs. Thus for most species at most kinds of flowers, the front legs are particularly important, being the primary pollen gathering structures. Pollen is generally transferred backward directly from the front legs to the middle legs (basitarsi), which also clean pollen from both dorsal and ventral surfaces of the thorax. However, these movements in the meliponine genus *Trigona* are unusual, as described below.

In flowers whose anthers are readily accessible, *Trigona* species commonly bite an anther repeatedly, loosening pollen, the antennae being bent down, their tips contacting the anther or nearly so. If there is already loose pollen, biting is unnecessary. At least *T. capitata, pallida, thoracica,* and *nigerrima,* and presumably all species, extend the proboscis, contacting the anthers repeatedly (Fig. 1). The pollen is presumably made sticky with nectar in this way, as is the case with *Apis.* As these activities continue, bees brush the anthers and especially the proboscis with the front tarsi, presumably accumulating pollen on the hairs of the basitarsi. The proboscis is scraped downward, toward its apex, with both forelegs (basitarsi?) synchronously. The pollen is then transferred by the front tarsi to an area of backward-directed, stiff hairs on the ventral surface of the mesepisternum in front of and between the middle coxae, and to similar hairs on the middle and hind coxae. These movements are synchronous, left and right forelegs moving simultaneously, the bee being supported by the middle and hind legs (Fig. 2). Moving pictures show that the fore tarsi are scraped forward across the coxal



FIGS. 1, 2. *Trigona nigerrima* taking pollen from *Hedychium*. In Fig. 1, in an interval between biting, the tip of the glossa is in contact with the pollen source and the forelegs are about to scrape the glossa and floral surface. In Fig. 2 the forelegs are transferring pollen to the thoracic venter and mid and hind coxae. These drawings are based on moving picture frames, but much detail has been added since they showed mainly silhouettes.

and mesepisternal vestiture to transfer pollen to the latter.

The behavioral repertoire of *Trigona* species must include somewhat different movements for flowers with loose pollen that does not need to be freed with the mandibles and that may be picked up by parts of the body and appendages other than the front tarsi. When *Trigona* species are foraging at flowers with abundant loose pollen that adheres to the body, it is no doubt brushed off of the different parts of the body by the inner surfaces of the basitarsi of all the legs. *T. pectoralis* and *T. (Paratrigona)* sp. collecting pollen on *Baccharis* (?) flowers had pollen densely caked on the inner sides of the hind basitarsi. Such pollen would never be transferred to the thoracic venter, but must pass directly to the corbicula. This is in contrast to our observations on *T. pallida* and *nigerrima* which had little pollen on the hind basitarsi.

POLLEN PACKING. We recognize two basic types of pollen packing in Apidae. Type I resembles the manipulation of nest materials, as described above, in that sticky masses are placed directly onto the corbiculae by the middle legs. In Type II, pollen is placed near the distal end of the corbicula rather than directly on the corbicular surface, and is then pushed basad into the corbicula. Special morphological features of the distal end of the hind tibia and base of the basitarsus are necessary for Type II pollen manipulation; these features differ among the groups of Apidae, as do the pollen-packing movements. There exists, therefore, various subtypes of Type II.

TYPE I POLLEN PACKING. It may be that all female apids retain, as part of their behavioral repertoire, pollen packing in which the middle legs place pollen directly into the corbiculae, as noted below for *Trigona (Trigonisca) buyssoni* and for *T. amalthea* on *Cucurbita*. For the former species this may be the principal method. It was observed on the same flowers where *T. nigerrima* was transferring pollen in the way more common for the Apidae (Type II). Most species probably use Type I packing only for large masses of sticky material such as resin, mud, or the large pollen masses of *Cucurbita*.

Trigona (Trigonisca) buyssoni bites the anthers of *Hedychium,* moistens the loosened pollen with nectar (?) from the glossa, and places it on the mesepisternum with the fore tarsi, as described above (under The Forelegs) in greater detail for other *Trigona* species. Then, while still standing on the anther or petal, supported by front and hind legs, the middle legs move pollen from the thoracic venter to the corbiculae. (The front legs could theoretically play a role in removing pollen from the thoracic venter, but if so, it must be one front leg at a time rather than synchronously since at least one front leg must support the body. Nothing of the sort was seen.) Movement of the middle legs is synchronous, and the pollen is scraped or patted onto the ipsilateral corbiculae by the middle basitarsi.

The abundant, coarse, sticky pollen of *Cucurbita* probably presents special problems or opportunities for bees collecting it. Our observations were made on *Trigona amalthea,* a form very close to and perhaps conspecific with *T. silvestriana* whose Type II handling of *Cassia* pollen has been observed by Wille (1963). But on *Cucurbita,* after several transfers of pollen (like those described under The Forelegs) from the anthers or from thick accumulations on the corolla beneath the anthers to the mesepisternum and adjacent coxae, the bee, while still in the flower and now supported by front and hind legs, uses the middle basitarsi to remove pollen masses from the mesepisternum and pat them onto the ipsilateral corbiculae. The result, after several such movements, is large but loose and irregular pollen masses on the corbiculae. The movements are similar to those of *T. postica* described by Sakagami and Camargo (1964) for placing cerumen on the hind tibiae for transportation. These movements make no use of the special structures (penicillum, rastellum) at the apices of the tibiae.

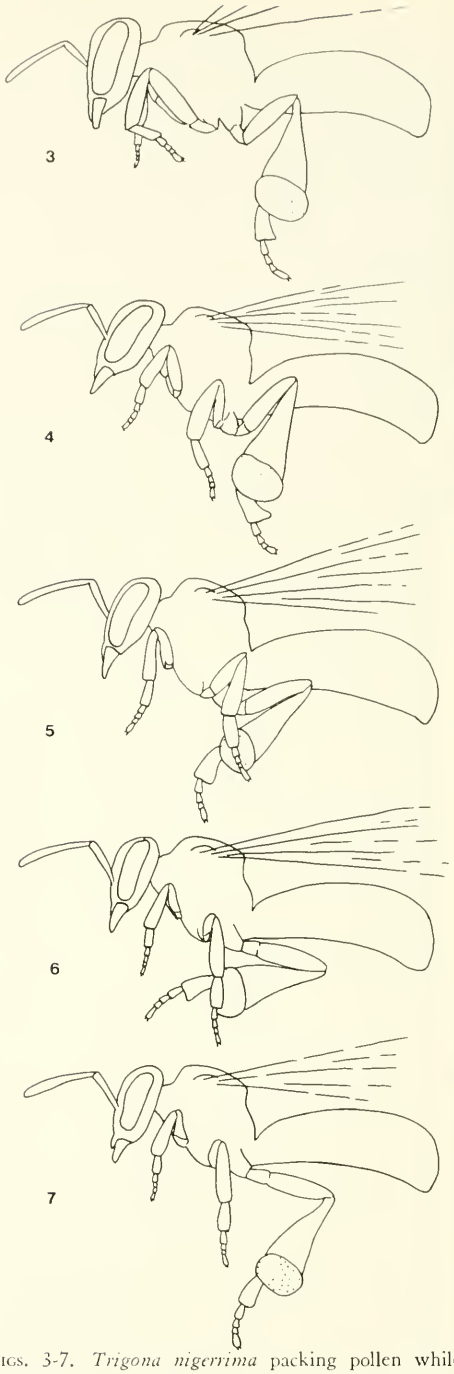
An old report (Hoffer, 1882) says that pollen is "pressed with the middle legs into the corbicula of the hind leg" by *Bombus.* This may indicate that Type I behavior is part of the repertoire of *Bombus,* as it is of other groups.

Even in *Apis mellifera,* when the corbicular pollen loads become large, the bee may pat them many times with the ipsilateral middle legs, probably to smooth and compact them. Some pollen may be added directly to the corbicular pollen masses in this way, although the quantity appears to be small (Parker, 1926).

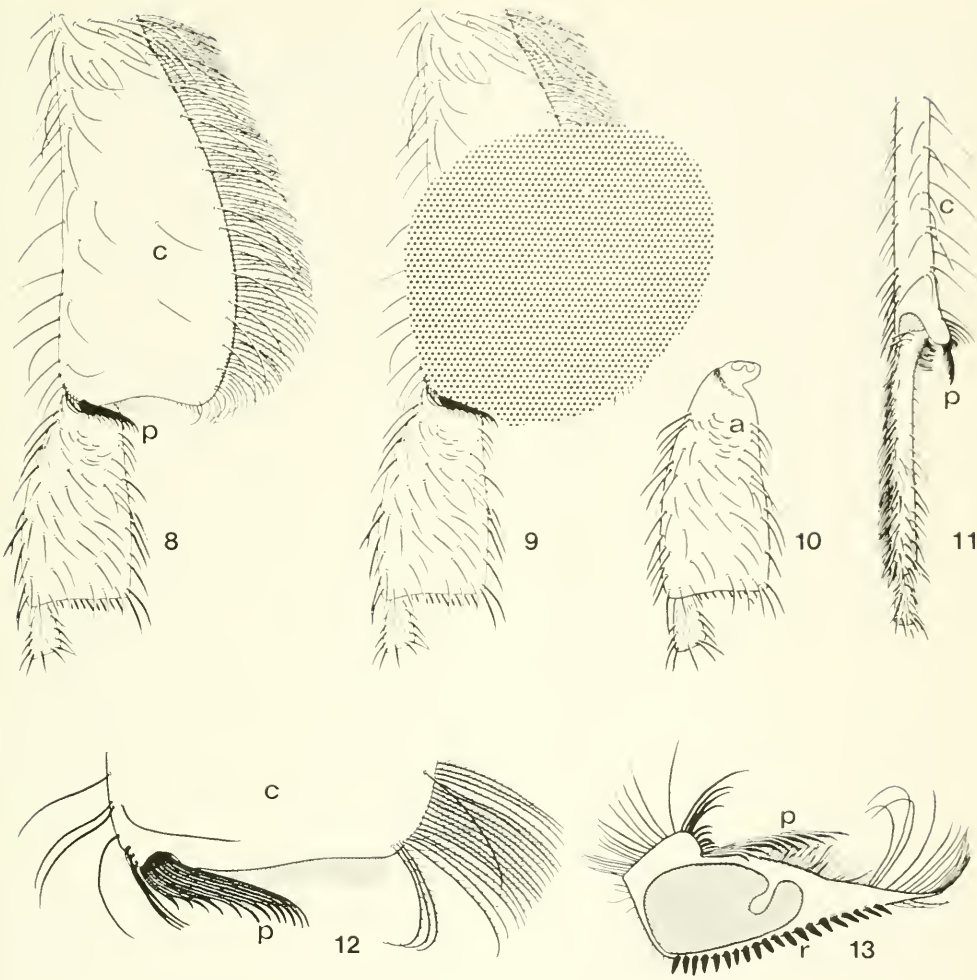
Type II Pollen Packing. This type of pollen packing involves (a) placement of sticky pollen in the region of the hind tibiotarsal joint by movements which depend upon the kind of bee and the kind of flower, and (b), most characteristically, pushing the pollen basad up the outer surface of the tibia from the region of the tibiotarsal joint. This movement of the pollen places it into the smooth and nearly hairless corbicula. This is unlike the filling of the scopa of other families of bees, where the dense scopal hairs prevent such a process, and it is unlike the Type I apid process in which pollen is placed directly into the corbicula by the middle leg. As described below, in *Apis, Bombus,* and probably the Euglossini, pollen is pushed basally into the tibial corbicula by the auricle, i.e., the broadened base of the basitarsus. As emphasized by Buttel-Reepen (1915), Maidl (1934), and Winston and Michener (1977), Meliponinae have no auricle. A major objective of this study, therefore, was to learn how Meliponinae fill their corbiculae.

Ipsilateral Type II Pollen Packing. Corbicular loading was observed for *Trigona pallida* and *nigerrima,* and has been briefly described for other species by Wille (1963) and Laroca (1970). After several foreleg movements that place pollen on the thoracic venter (Figs. 1 and 2), the bee

takes wing, thus freeing the middle and hind legs of their supporting function and enabling them to make pollen-transferring motions. While the bee is hovering, the middle legs synchronously rotate far forward (Fig. 3) and may scrape backward over the thoracic venter, removing pollen from the hairs of that area. However, in their far forward position they hide the front legs so that it is difficult to see, and photographs do not show, whether or not the front legs first remove the pollen from the mesepisternum and transfer it to the mid legs, as stated by Wille (1963) and Laroca (1970). Our impression from the moving pictures is that both may happen, the forelegs scraping pollen perhaps from median ventral areas for transfer to the mid legs, and the latter removing pollen from the lateroventral areas. In any event the mid legs quickly rotate back (Fig. 4) from a far forward position to a backward position and transfer pollen to the ipsilateral hind legs. At first the mid tibia and tarsus come back almost parallel to the hind tibia (Fig. 5), but then the hind leg is flexed forward (Fig. 6) so that the mid basitarsus lies across the outer surface of the tibia or the tibio-basitarsal joint of the hind leg, at right angles to the long axis of the hind tibia. The movement of the hind leg is especially noticeable in hovering *T. clavipes* and *nigerrima* because of the long and dark posterior legs, but it occurs in all species and is necessary if the contact is to be at right angles to the hind tibial axis. The position of the mid leg against the outer surface of the apex of the hind tibia shows repeatedly in our moving pictures of *T. nigerrima* hovering while manipulating pollen. Straightening of the hind leg (Fig. 7) and to a minor extent, simultaneous forward movement of the mid leg combine to scrape the pollen-carrying mid basitarsus across the apex of the hind tibia. The photographs show that sometimes the mid basitarsus is also



FIGS. 3-7. *Trigona nigerrima* packing pollen while hovering near *Hedychium* flowers. Fig. 3, Mid leg has removed pollen from thoracic venter or possibly foreleg. Fig. 4, Mid leg moving quickly backward. Fig. 5, Mid leg over pollen mass (dotted) on hind leg. Fig. 6, Hind leg bent forward so that mid leg lies across tibiotarsal joint. Fig. 7, Hind leg straightened and mid leg moved forward, pulling mid tarsus across hind leg. Drawings prepared as for Figs. 1, 2.



FIGS. 8-13. Hind leg of worker of *Trigona pallida*. Fig. 8, Tibia and basitarsus. Fig. 9, Same with large pollen mass. Fig. 10, Basitarsus showing basal structure. Fig. 11, Tibia and basitarsus in anterior view. Fig. 12, Apex of tibia, outer view. Fig. 13, Distal view of apex of tibia. p, penicillum; r, rastellum; a, auricular area; c, corbicula.

seemingly pressed against the pollen mass in the corbicula. This could be either adjustment of the pollen mass or a Type I addition of pollen, but the arrangement of pollen from different sources suggests the former (see section on The Corbicular Pollen Load in Meliponinae).

The pertinent hind tibial and basitarsal structures of *Trigona pallida* are shown in Figures 8 to 13. The penicillum is a row of stiff bristles arising on the lower (or anterior) distal angle of the tibia. They sweep upward (or posteriorly) parallel to the tibial apex, but well separated from it, and then curve distad at their tips. The longest bristles are the outermost while those nearer the corbicular surface are progressively shorter (not true of all species). The hind basitarsus except at its tibial articulation is offset mesally (Fig. 11), so that there is a gap between its outer surface and the curved apices of the bristles of the penicillum. The structure suggests that through this space the ipsilateral middle basitarsus is drawn at right angles to the long axis of the hind tibia in order to transfer pollen onto the latter. The apices of the penicillar bristles would scrape the

pollen out of the hairs on the outer surface of the mid basitarsus, and the penicillar curvature, during posterior movement of the hind tibial apex relative to the mid basitarsus, would force such pollen basad onto the outer surface of the tibia. The progressive shortening of the penicillar bristles from the outer to the inner ones makes the comb oblique, tending to push the pollen against the apex of the corbicula. Thus the movement of hind leg relative to the middle could alone be responsible for pushing some pollen basad into the corbicula.

The posterior basal area of the outer surface of the hind basitarsus is provided with hairs which are directed posterobasally (Fig. 10), not apically like most other hairs. We speak of this part of the basitarsus as the auricular area because of its location, comparable to that of the auricle of other subfamilies of Apidae. The hairs of the auricular area often have some pollen on them and presumably serve to scrape pollen off of the inner hairs of the ipsilateral middle basitarsus. Laterad movement of the hind basitarsus would press the mid tarsus between the penicillum and the posterior basitarsus itself (including the auricular area) as the hind tibial apex is moved backward relative to the mid leg. Posterior flexion of the hind basitarsus would then help to push pollen that comes off onto the auricular area up onto the corbicula, thanks to the direction of the hairs in that area.

As repeated passages of the mid basitarsus add pollen to the distal end of the ipsilateral outer tibial surface (supplemented by the pollen from the inner surface of the contralateral hind basitarsus, see below), the added pollen must pile up and be pushed basally. The motive forces are presumably the scraping movement of the hind leg along the mid leg as already described, supplemented by back and front (up and down) flexions of the basitarsus. Examination of freshly killed pollen collectors of *Melipona* and *Trigona* frequently show pollen on the tibial apex in the space between the inner side of the penicillum and the outer sides of the basitarsus and rastellum. In *T. pallida* a small brush (Figs. 10 and 11) arising along a curved line on the basal part of the auricular area, behind the penicillum, can, with backward flexion of the basitarsus, push such pollen basad onto the corbicular surface. It consists of weak hairs hardly able to move the whole pollen mass, but its effectiveness with small amounts of pollen was shown by drawing a detached middle tarsus with pollen on it through the gap described above (between the penicillum and the hind basitarsus) on the hind leg of a freshly killed worker of *T. pallida*. Part of the pollen was combed off as expected by the penicillum, but the quantity was not enough for the curvature of the penicillum to push much pollen basad onto the corbicula. The basitarsus was then flexed backward, with the result that the brush moved the pollen onto the distal end of the corbicula where it remained, held by its stickiness. In *Melipona,* as in most *Trigona,* there is no defined brush, but rather a hairy auricular area (Fig. 14) with hairs directed posterobasally, as described above. The frequent presence of small amounts of pollen on this area in *Melipona* and *Trigona* suggests its importance in pushing pollen upward. Such movement is possible because of the highly flexible tibiotarsal joint, activated at least in *Apis* (Snodgrass, 1956) by three muscles.

A casual observer might suspect from the curvature of the penicillar bristles that the penicillum must somehow function as a scoop, accumulating material on its concave surface. Actually if our interpretation is correct, the penicillum scrapes pollen onto its convex surface. Like the rastellar bristles in *Apis,* the penicillar bristles comb in the direction of the apices of the hairs

from which they are removing pollen. Such scraping movements can remove indefinite amounts of pollen because new pollen easily pushes away that already present. This would not be the case for a scoop.

Contralateral Pollen Packing in Apis *and* Bombus. Although it largely occurs while the bees are in flight, the process of pollen manipulation and packing onto the corbiculae for transport has been studied repeatedly for *Apis* (for references, see Ribbands, 1953; Snodgrass, 1956, and Legge and Bole, 1975). Sladen (1912a) and Buttel-Reepen (1915) found the process for *Bombus* to be similar, and the structures involved in *Apis* and *Bombus* are remarkably similar. The following comments are based primarily on published material on *Apis mellifera.* The bees gather pollen from their hairy bodies or from anthers by movements of the legs. At the same time, they may moisten it with nectar, making it sticky. The basitarsi bear the primary brushes involved. The front basitarsi brush both anthers and the proboscis, the latter adding nectar and making the pollen sticky. These basitarsi also brush the head and front of the thorax. R.J. observed *Apis* workers taking pollen from flowers of *Cytisus* directly with the middle, rather than the front tarsi, and bees on flowers with loose pollen will have accumulated pollen on most parts of the body and legs. The bee now leaves the flower and hovers. Pollen on the front basitarsi is transferred to the middle ones, which also scrape pollen off of much of the thorax both dorsally and ventrally. The middle basitarsi, one at a time (Beling, 1931), are now scraped between the inner sides of the apposed hind basitarsi. These basitarsi also scrape pollen off of the abdomen. The hind legs are rapidly rubbed against one another in a pumping motion. In this process the rastellum scrapes distad, removing pollen from the inner surface of the contralateral basitarsus. The pollen accumulates on the posterior basal projection (auricle) of the basitarsus or between the auricle and the rastellum. Then, by posterior (upward) flexion of the basitarsus, the auricle forces pollen basad onto the corbicula. Repetition adds more and more pollen at the distal end of the corbicula, forcing the first pollen collected toward the base of the tibia and ultimately filling the entire corbicula with pollen, which may also be patted from the outside by the ipsilateral mid basitarsus, as noted in the section on Type I Apid Pollen Manipulation. It seems possible that the latter movement may also add some pollen directly from the mid legs to the corbiculae. In both *Apis* and *Bombus,* however, pollen loads composed of different colored pollens from different flowers show that the material is added from the apex of the tibia (Buttel-Reepen, 1915).

Because the published information on *Bombus* is largely presented only by indicating the similarity to *Apis,* R.J. made observations and moving pictures of workers of *B. pennsylvanicus* collecting pollen from *Cassia.* While incomplete, these studies generally verify and supplement the observations made early in the century by Sladen and Buttel-Reepen. A *Bombus* takes a position ventral side up under an inverted flower, usually hanging by its forelegs, sometimes with the midlegs also on the flower. This is clearly a special position for extracting pollen from flowers like those of *Cassia* with tubular anthers. The forelegs do not perform their usual pollen-collecting function and the mid and hind legs are probably freer than usual for pollen-manipulation movements usually performed in flight. The hanging bee produces rhythmic buzzing sounds—vibrations which no doubt release the pollen through the openings in the apices of the anthers (Michener, 1962; Wille, 1963). The pollen falls onto the underside of the bee and especially onto the venter of the abdomen.

While the bee is hanging from the flower, the hind legs (probably under sides of basitarsi but possibly the rastella) sweep back and forth (scraping or rubbing, we cannot say which), transversely, synchronously, removing pollen from the abdominal sterna. In each such movement, as they approach the midventral line of the abdomen, the distal parts of the tarsi meet and interfere with the process. The result is a longitudinal, midventral line of pollen, not swept up by the basitarsi or tibiae.

While still hanging from the flower, the bee performs at least five movements with the middle legs. They were observed to occasionally groom a foreleg by flexing so that the foreleg is scraped simultaneously by mid femur and basitarsus. (This familiar movement is presumably functionless for pollen collecting in the context of *Cassia* flowers.) Midlegs more often scrape anteriorly on the dorsum of the thorax and posteriorly on the venter between fore and mid coxae. The latter movement should sweep *Cassia* pollen from the thoracic venter. The middle legs also, one at a time, extend backward, are appressed between the hind basitarsi, then pull forward as the hind legs are straightened backward. This scrapes pollen from the middle basitarsus onto the under sides of the hind basitarsi. (Basitarsi of pollen-collecting individuals of *Bombus cayennensis* had abundant pollen on their under surfaces.—C.D.M.) Finally, midlegs occasionally pat the corbicular pollen loads, usually starting at the basal part of a pollen mass and working toward the distal part.

Bombus in flight were photographed while cleaning the forelegs with the midlegs and the midlegs with the hind legs—movements also seen while bees were hanging from flowers. In addition, film analysis revealed pumping movements of the hind legs like those described for *Apis*. It was verified that the hind basitarsi are not pressed against one another as during grooming; contact is in the vicinity of the tibiotarsal joint and we believe that the rastellum of each tibia combs pollen from the underside of the opposite basitarsus. This would lead to deposition of pollen on the auricle, which would push it into the distal end of the corbicula, just as in *Apis*.

Contralateral Pollen Packing in Meliponinae. Although Meliponinae lack auricles, most of them have rastella; it was therefore natural to look for contralateral corbicular loading similar to that known for *Apis*. In some species of *Trigona,* contralateral pollen packing is of little importance, at least at the flowers where we made our observations. Thus the hind basitarsi of *Trigona nigerrima* and *pallida* are brought rather close to one another beneath the body during pollen loading, so that the middle legs can be drawn across the outer surfaces of the hind legs, as described in the section on Ipsilateral Type II Pollen Packing. The hind legs may touch one another and make some basad-distad alternate pumping movements. Moving pictures of hovering *T. nigerrima* taken from the rear show occasions when the inner apex of a hind tibia, bearing the comb or rastellum, combs downward over the inner surface of the opposite or contralateral basitarsus, followed by the same movement of the opposite leg. This alternating or pumping movement is probably not important for pollen manipulation in the cases most intensively studied, *Trigona pallida* on *Ipomoea* and *T. nigerrima* on *Hedychium,* for in these cases the pollen was picked up as described above, exclusively by the front legs; little or no pollen got onto the abdomen or hind tarsi. Moreover, pollen was rarely found on the inner sides of the hind basitarsi in the pollen-collecting bees, and when present, there was but little. The pumping movements in these instances were probably cleaning

or self-grooming activity or stereotyped activity that may have importance in pollen manipulation at other kinds of flowers. These species, however, like all others in the subgenus *Trigona* and certain species of the subgenus *Tetragona,* have a large sericeous area, not covered with bristles, on the inner side of the hind basitarsus. Such a basitarsus must be inefficient, compared to that of other Apidae, in brushing pollen from the middle tarsus and therefore in contralateral pollen packing.

The other subgenera of *Trigona,* like other Meliponinae, have the underside of the hind basitarsus fully bristled and it is among such forms that contralateral pollen packing is most likely to occur. As noted above, much pollen was found on the inner sides of the hind basitarsi of *T. (Scaptotrigona) pectoralis* and *T. (Paratrigona)* species collecting pollen on *Baccharis* (?). The species of *Scaura* discussed in the nest section must depend largely on contralateral pollen packing. More significantly, there was much pollen on the inner sides of the hind basitarsi of *T. (Cephalotrigona) capitata* and *T. (Paratrigona) impunctata* collecting pollen from *Stylosanthes,* even though this is a small-flowered legume whose pollen was being removed from the flowers by the front tarsi only. Thus, unlike *Scaura* and the bees on *Baccharis,* those on *Stylosanthes* were not getting pollen on the body. Pollen must have been actively transferred to the inner sides of the hind basitarsi.

Behavioral observations, while not decisive, indicated the same conclusion. Pollen collectors of *T. capitata,* at least those with large pollen loads, seem to place the mid tarsi between the hind tarsi while hovering, after visits to one to several flowers. Thereafter distad-basad pumping movements of the hind legs were conspicuous, the inner apices of the tibiae apparently scraping the inner surfaces of the basitarsi. Sometimes, however, the mid basitarsi appeared to be outside the hind tibia, which (together with the presence of a strong penicillum) suggests that ipsilateral packing also occurs. *T. (Paratrigona) impunctata* is too small for detailed observations while hovering, but it very rarely seems to transfer pollen while resting on a flower. One mid tarsus at a time is extended posteriorly and pulled forward between the two hind basitarsi which are held with their inner surfaces apposed. This movement was seen performed by two pollen-collecting individuals. The only problem in its interpretation is that this is a typical apoid cleaning movement. The observer (C.D.M.) believed that the movement was pollen transferral, but recognized that it could have been merely cleaning of the middle tarsus. It was followed by hovering and pumping movements of the hind legs, suggesting pollen packing.

Aside from the bristles on the inner side of the hind basitarsus, an essential structure for contralateral pollen packing is the rastellum. This is a row of bristles (Fig. 13) along the inner margin of the apex of the posterior tibia. In *Apis* and *Bombus* the rastellum functions to comb pollen off of the inner surface of the contralateral hind basitarsus, and it extends more or less the full width of the tibial apex. In Meliponinae the row of bristles is commonly shorter, being largely posterior to the basitarsal articulation and penicillum, but probably has the same function; the pumping motion of the hind legs involves combing of hind basitarsi by the rastella. The result is accumulation of pollen from the contralateral basitarsus on the apex of the tibia lateral to the rastellum, from which location basitarsal movements combined with the hairs of the auricular area can presumably push pollen basad onto the corbicula, as in the case of ipsilateral pollen packing.

Probably another significant function of the rastellum is as a fence to prevent

the pollen that is transferred to the outer surface of the hind leg from being pushed onto the inner surface in the course of the tarsal movements. Even if, as in the *Trigona pallida* and *nigerrima* which we studied, little or no pollen is coming from the inner surfaces of the hind basitarsi, pollen arriving on the outer side of the tibiotarsal area might leak through and be lost on the inner surface of the hind tibia in the absence of a rastellum.

The Corbicular Load in Meliponinae. Since in both ipsilateral and contralateral pollen-packing movements, pollen is placed at approximately the hind tibiotarsal joint, there must be a mechanism for forcing pollen basad from that area into the corbicula. This mechanism has been described above, and it is reassuring that pollen loads collected from two or three different kinds of flowers by *Melipona fasciata, M. favosa,* and *Trigona fimbriata* indicate the existence of such a mechanism. The pollens in all such loads are arranged as though each new kind were added from the distal end of the tibia (Fig. 14), pushing previously acquired pollen basad over the corbicular surface. If successive kinds of pollen were patted onto the surface of the load (Type I), the different kinds would constitute shells one over the other; this is not the case. In other apid subfamilies the auricle of the basitarsus plays an essential role in pushing pollen basad into the corbicula but, as noted before, the Meliponinae have no auricle.

As the pollen mass on the meliponine corbicula enlarges, it is held and supported by the erect hairs of the lower (or anterior) corbicular margin, by the erect "outer penicillum" or parapenicillum of species such as *Trigona pallida,* by the penicillum proper, and by the few curled hairs at the distal end of the posterior margin of the tibia. The long upper (or posterior) fringe of the corbicula in most *Trigona* species, however, does not contain more or less

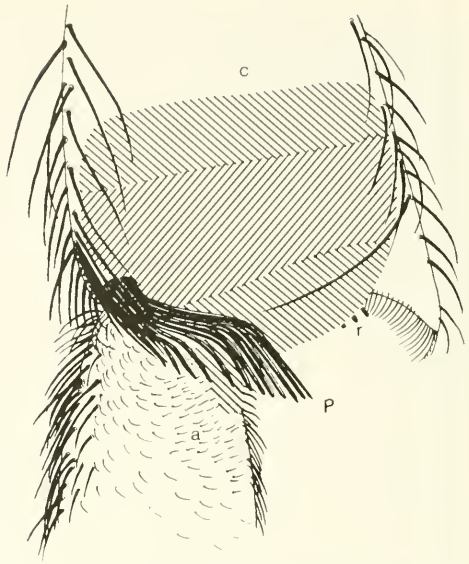


FIG. 14. Apex of tibia and base of basitarsus of *Melipona fasciata,* worker, showing by shading positions of different kinds of pollen. Abbreviations as for Figs. 8-13. Note the pollen on the auricular area behind the penicillum.

erect or curled hairs that enclose a corbicular space, as in *Apis, Bombus,* and *Melipona,* but extends posteriorly from the corbicular surface. The pollen mass moves partly out over these hairs (Fig. 9) and the stickiness of the pollen and the liquid incorporated with it holds the pollen both to the corbicular surface and to the posterior fringe of hairs. The pollen mass may be shaped to some degree, or adjusted, by patting movements of the middle legs.

Specializations of Meliponine Pollen Collecting. There doubtless exist, within the behavioral repertoire of various meliponine bees, many modifications of the patterns described above. Wille (1963) describes how *Trigona f. fulviventris, fuscipennis,* and *silvestriana* cut holes in the tubular anthers of *Cassia biflora* and extract pollen from them with the glossa. Laroca (1970) indicates that *T. spinipes* and *subnuda* behave similarly with similar tubular *Tibouchina* anthers, while *T. fulviventris guianae* cuts the tips off of the *Tibouchina* anthers and then exploits them in the same way.

Similar observations were made by C.D.M. at flowers of another melastomaceous shrub in French Guiana. The flowers are managed differently by different meliponine bees, as follows: *Melipona pseudocentris* curls the body over the group of anthers and buzzes, receiving the pollen from the tubular anthers on the under side of the body as described for other bees by Michener (1962) and Wille (1963). *Trigona impunctata* chews the basal thick parts of the anthers open and extracts pollen with the glossa and fore tarsi. *T. fulviventhis guianae* chews off the attenuate distal parts (one third to one half) of the anthers, thus providing an entrance much larger than the small apical pore, and reaches in to extract pollen with the glossa. It then scrapes pollen off of the tongue wth simultaneous distad movements of the front basitarsi. A single bee often cuts the apices off of most or all of the anthers in a flower before going on to another.

Trigona species sometimes are gleaners, picking up pollen from corolla surfaces where it falls following visits to anthers by other insects. Although the pollen on the surfaces is usually invisible, bees collect large pollen loads on the corbiculae from these sources. Wille (1963) described such behavior for *T. jaty, nigra,* and *testaceicornis* on *Cassia biflora*. On another *Cassia species* C.D.M. and M.L.W. observed that *T. impunctata* visited only the anthers, biting them to get pollen, and *T. pallida* usually did the same thing. The latter species, however, was sometimes also a gleaner, going over the corolla surface below the anthers with the antennal tips down to the surface, the glossa slightly excerted, and the mandibles moving; the fore tarsi swept up the pollen, especially by scraping distad on the glossa, to which it probably stuck because of regurgitated nectar. The rest of the manipulation for both *T. impunctata* and *T. pallida* was as described previously.

The subgenus *Scaura* of *Trigona,* however, appears to consist of specialized gleaners and visitors to inflorescences consisting of relatively broad surfaces from which pollen can be swept up. These bees have extraordinarily large and hairy hind basitarsi (also hairy middle basitarsi), the principle subgeneric characteristic. Laroca and Lauer (1973) describe pollen collecting by *T. (S.) latitarsis* from the cylindrical inflorescences of *Piper* and from the leaf surfaces beneath the flowers of *Amaranthus*. They describe the use of the hind basitarsi for sweeping up pollen and the rubbing of the hind legs against one another, as described below for *T. longula*. *T. latitarsis* is a minute bee, undoubtedly difficult to observe. From its morphology, we assume that its behavior is similar to that of *T. longula,* a larger species for which we obtained fuller, although still incomplete, information on pollen manipulation.

Trigona longula was visiting a large-flowered *Cassia* species. Only rarely do these bees go to the anthers. When they do, they collect pollen and manipulate it, so far as we could see, like other species of the genus. Nearly all the pollen collecting was by gleaning from petal, bud, or leaf surfaces below the anthers. (Flowers were visited by *Xylocopa, Eulaema, Euglossa,* and *Centris,* whose buzzing releases pollen, as shown by Wille, 1963.) On such surfaces, there was no noticeable deposit of pollen, but individuals of *T. longula* were able to fill their corbiculae there. In ordinary walking, *T. longula* moves like any other *Trigona* species. On polleniferous surfaces, however, the middle and hind legs are splayed out, the inner surfaces of the basitarsi against the substrate, the hind basitarsi bent forward almost at right angles to the body even though the femora and tibiae are directed backward. With the legs in this position, the bee shuffles

along, dragging the distal part of the abdomen. The tips of the antennae are bent down to the surface; the front legs perform ordinary walking movements. The basitarsi and abdomen must pick up pollen from a rather broad swath as the bee moves along.

A collecting bee frequently stops, raises its abdomen, and while supported by fore and mid legs, scrapes backward over the abdominal surface synchronously with the inner surfaces of the hind basitarsi. Then, beneath the abdomen, it rubs or scrapes the inner surfaces of these basitarsi against one another or the apices of the tibiae in the course of pumping movements of the hind legs. Then the hind legs are lowered for support and the middle legs are brought back usually synchronously to the regions of the apices of the hind tibiae, and the mid basitarsal regions are pulled forward across the outer surfaces of the apices of the ipsilateral hind tibiae. This seems to be a shorter movement than in *T. pallida,* perhaps because the hind legs are not moveable, being used in support, and is oblique, not at right angles to the tibia.

Less often the bee hovers and transfers pollen to the corbiculae by means of leg movements that appear to be similar to those of other *Trigona* species. Details, however, could not be discerned.

Microscopic examination showed that the underside of the apical part of the abdomen (metasomal sterna 4 and 5) has hairs which are curved downward at their apices and thus should readily pick up pollen as the abdomen is dragged forward across the substrate. The inner surfaces of the mid and hind basitarsi are unusually hairy. The outer surface of the broad hind basitarsus is swollen, convex except for the broadly concave auricular area (Fig. 15). The rastellum is long for a meliponine bee.

From these observations we suppose that pollen collected on the inner surface

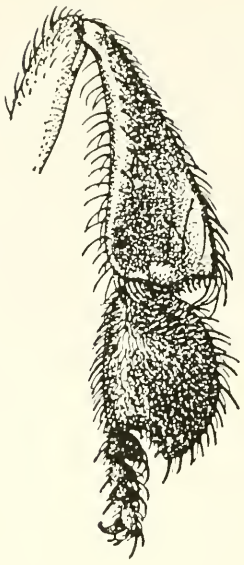


FIG. 15. Hind tibia and tarsus of worker of *Trigona (Scaura) longula* (modified from Schwarz, 1948).

of the hind basitarsus, both from the substrate and from the abdomen, is combed off that surface by the contralateral rastellum during the observed pumping movements. Pollen should pile up outside of the rastellum; freshly killed pollen collectors had pollen between rastellar bristles and on the outer rastellar surface. Then the concave auricular area, functioning like the auricle in other groups of apids, presumably pushes pollen up into the corbicula. The unusual width of the hind basitarsi, their use and that of the abdomen for pollen collecting, and their general outer convexity so that a concave auricular area can be present, all suggest that contralateral pollen transfer from the inner sides of these basitarsi is more important than in most *Trigona* species. Pollen collected by the front and middle legs is manipulated ipsilaterally, to judge by the observations described above, the penicillum and auricular hairs combing it off and directing it up into the corbicula. We saw no evidence of pollen being removed from the hind legs by the middle legs for transfer to the corbicula, as indi-

cated by Laroca and Lauer (1973) for *T. latitarsis.* As this would involve a forward movement of material, something not seen in grooming or pollen handling behavior of any other bees (Jander, 1976, and in preparation), we suspect an observational error. This would not be surprising considering the minuteness of *T. latitarsis.*

The Euglossini. Pollen collecting by *Euglossa* near *cordata* and *ignita* was observed on small tubular flowers *(Sabicea)* that served also as a nectar source. Hairs on the basal part of the proboscis pull pollen out of the flower. When a bee rears back to withdraw the long proboscis, it places the front tarsi (basitarsi?) on either side of the proboscis, scraping distad several times with the front legs, thus presumably removing pollen from the proboscis.

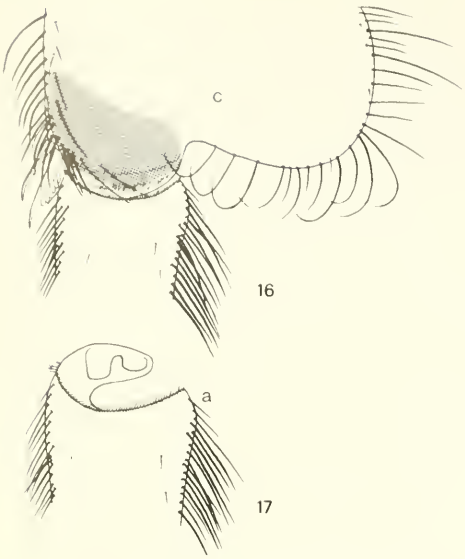
While this is going on the epipharynx, which is extraordinarily long in Euglossini, is exerted and probably adds nectar to the pollen. The proboscis, used for this purpose in other apids, is so long in Euglossini that it could scarcely have this function.

The bee then takes wing and hovers, or rarely grasps a leaf edge with its mandibles and hangs. In either case, the middle and hind legs are freed of their support function, so as to allow pollen manipulation, which is rapid and difficult to observe.

The front legs come back synchronously and apparently the tarsi are scraped by the basitarsi of the flexed middle legs, in the usual way. The latter then moved back synchronously to contact the hind legs. At least part of the time the mid leg pats the corbicula and pollen load on the outside of the ipsilateral hind tibia. Rubbing of the inner surfaces of the hind legs one on the other (pumping motion) was also probably observed; certainly such motions were visible, but contact between the two hind legs could not be verified.

Examination of various females of *Euglossa, Euplusia,* and *Eulaema,* killed while collecting pollen, provided more information. The front legs often had a little pollen on the inner surfaces of the basitarsi and less on the tibiae, more on the posterior margins of the inner basitarsal surfaces than elsewhere. The middle legs had similarly distributed pollen, even more predominantly along the posterior margins. Presumably it is the hairs of the posterior parts of the inner surfaces that transfer much of the pollen. On the hind legs, there is little or no pollen on the inner surfaces of the tibiae or tarsi, except that when the pollen load is very large, a thin and broken layer may be present on the inner surfaces.

Whenever the pollen load is of moderate or small size, pollen on the tibiotarsal articular region is limited to the area of the rastellum, and it is on the outer side of the row of bristles, not on the inner side. On the corbicula, any small pollen load is always immediately above the base of the basitarsus, as shown in Figure 16. It must be pushed up to this position by the auricle at the posterior base of the basitarsus. The auricle is present, but unlike that of *Apis* and *Bombus,* it is close against the tibial apex, which is so shaped that the base of the basitarsus rides over the convex tibial apex as the tarsus is moved relative to the tibia. When the pollen load is slightly larger, as in most specimens examined, the small fringe at the anterior base of the basitarsus seems to have played a role (Figs. 16 and 17). This fringe must push pollen among the hairs of the anterior corbicular fringe, for they are surrounded by pollen. Thus if the tarsus is flexed backward, the auricle pushes pollen basad, while if it is flexed forward, the anterior basal fringe does so. There is often some pollen on the outer side of the basitarsus, but this is discontinuous with that on the corbicula except when the pollen load is



FIGS. 16, 17. Structures of hind leg of female of *Euglossa ignita*. 16, Apex of tibia and base of basitarsus, showing by shading location of a small pollen load. 17, Base of basitarsus of same, showing auricle at right and small fringe at upper left that may play a role in moving pollen.

enormous. The movement of the auricle over the bulla or convexity of the tibial apex readily causes this discontinuity.

All this supports the observation that the pollen is applied to the outer surface of the hind leg near the tibio-tarsal joint by the middle leg. Apparently the rastellum serves primarily as a fence to keep the pollen from "leaking" through onto the inner surface. In any event, the rastellum seems to be so positioned that it could comb the contralateral basitarsus only with difficulty. Finally, the huge pollen loads often attained, especially by *Euplusia* and *Eulaema*, are made possible partly by the enormous, posterior expansion of the tibia and could hardly be managed except with adjustment and shaping by the middle legs; some pollen is likely to be added directed to the pollen load in this way.

EVOLUTIONARY CONSIDERATIONS

EVOLUTION OF POLLEN COLLECTING AND TRANSPORT. In the evolution of pollen-carrying behavior, three successive basic phases can be recognized. If Jander (1976) is correct in considering the crop as the ancestral pollen-carrying structure, the pollen-collecting behavior of *Hylaeus* illustrates the first phase, utilizing structures and behaviors already present in the Sphecidae. *Hylaeus* carries pollen in the crop, collecting it by brushing it off the anthers with the forelegs and then scraping it off each foreleg with a comb on the maxillary galea (Jander, 1976). There is also the possibility that *Hylaeus* eats pollen directly. Moreover, *Hylaeus* can scrape the head with the forelegs and then eat the pollen that was lodged on the head. There are no known *Hylaeus* movements for transferring pollen from the thorax or abdomen to the mouth; such pollen is wasted or the small amounts that stick to the body surfaces are brushed off in a cell, if our knowledge of the repertoire of movements is complete (Jander, in preparation). This *prototypic pollen collecting* of *Hylaeus* persists into the major evolutionary lines of the bees, even though most pollen transport in such bees is external.

In the evolutionary line that led to the families Anthophoridae and Apidae, the original galeal comb of the primitive bees is replaced by a stipital comb (Schremmer, 1972; Jander, 1976), although in many taxa there is no maxillary comb. Within the Apidae a well developed stipital comb is present only in *Bombus* and only *Bombus* is known to have the prototypic pollen-collecting behavior of scraping pollen off of the forelegs with the mouthparts (Jander, 1976). Most other Apidae, including *Apis*, however, have weak stipital combs.

The second phase of the evolution of pollen-collecting behavior led to *eutypical pollen gathering* and transport in a scopa on the hind legs as in the majority of the bees. In eutypical pollen gathering, pollen is transferred from the flower into a scopa

on the hind legs; as noted in the Introduction, it is passed from the anthers to the scopa via the foreleg and the middle leg.

Eutypical pollen manipulation is characteristic (with minor modifications) of at least Colletinae, Halictidae, Andrenidae, and Anthophoridae (including Xylocopinae), of course with the exception of parasitic forms in such groups. Most bees of these groups have hairy bodies on which loose pollen lodges as they work in flowers. Since the middle legs can scrape the thorax as well as the front legs, these bees have movements whereby pollen can be transferred from both the head (as in *Hylaeus*) and the thorax to the scopa. (In many Anthophoridae, scraping movements of the forelegs clean the dorsum of the thorax; Jander, 1976.) Eutypic pollen manipulation should be more efficient than prototypic. However, the eutypical movements still cannot transfer pollen from the abdomen to the scopa. All bees scrape the abdomen with the hind basitarsi to clean it, but pollen on the abdomen must be either lost or merely brushed off in a cell. Type I pollen packing as described above for Apidae is a modification of eutypical pollen transport behavior.

Eutypical pollen gathering has been supplemented by or transformed into a variety of different *metatypic or derived pollen gathering* and transport methods. For example, in the Megachilidae the scopa on the hind leg is replaced by one on the ventral side of the abdomen. The pertinent pollen-gathering movements are only partially known (Michener, 1953), but appear to differ from eutypical movements in that the hind legs transfer pollen to the scopa. As they can also brush the abdomen, megachilids should be able to transfer to the scopa for transport, pollen lodging on almost any part of the body. Within the Apidae pollen transfer movements onto the middle leg are also not noticeably different from those of eutypical pollen gathering (except in the genus *Trigona*). The derived pollen handling features are largely restricted to the interactions between middle and hind legs and pollen packing from the distal end of the tibia. In other words, Type II pollen packing is among the derived methods.

The derived or metatypic movements found in most Apidae include scraping of the abdomen with the inner surfaces of the hind basitarsi and transfer of this pollen to the contralateral corbiculae for transport. Thus, pollen that lodges from flowers on the abdomen, as well as that on the head and thorax, can be used. Derived movements also include transfer of pollen from the middle legs to the inner surfaces of the hind basitarsi. They clearly include the pumping movements of the two hind legs in which the rastellum scrapes pollen off of the contralateral hind basitarsus onto the basal surface of the auricle, and movements of the basitarsus which push pollen basad into the corbicula, which is thus loaded from its distal end. These matters are described in detail above in the section on Type II pollen packing.

Evolution of Corbiculae and their Filling Mechanisms. The Apidae have a corbicula on the hind tibia and for all subfamilies of the Apidae it is known that at least sticky material can be transferred into the corbicula in the eutypical behavioral sequence, described above in the sections on Type I Pollen Packing and Transport of Nesting Materials. Hence the corbicula and the eutypical behavioral sequence must have existed in a common ancestor of all Apidae. In the Introduction we suggested the development of the corbicular scopa from the brushy tibial scopa of Anthophoridae. We have two theories, not mutually exclusive, to account for the origin of corbicular transport as contrasted to transport among the hairs of a brushy scopa. One is that a single stroke

of the mid leg is sufficient to empty a corbicula, while several strokes must be needed to empty a brushy scopa. The former should be more efficient. The other theory is that the corbiculae arose in connection with the use of sticky materials for nest construction. It is true that some Megachilidae use resin, mud, and other sticky substances for making cells, but they do not transport such materials in the scopa. It is also true that in the Anthophoridae there are forms such as some *Centris* which transport oil (Vogel, 1974) or mud (Michener and Lange, 1958) in the scopa. However, it seems that it would be nearly impossible to remove highly sticky materials like gums and resins from a brush of dense and usually branched scopal hairs (although Roubik and Michener, in press, indicate that this happens in *Epicharis*). Winston and Michener (1977) therefore suggested that the smooth corbicular surface serves to facilitate removal of such material from the hind legs in the nest, after transport. Most Apidae use the corbicula for transport of both construction materials and pollen. As the corbiculae, according to this theory, are adaptations for the transport of sticky material, it is not surprising that these bees make the pollen into a sticky material too, by the addition of nectar as it is collected.

Because a corbicula can be filled with sticky material in the eutypical fashion and because it is mechanically impossible for a brushy scopa to be loaded with pollen by the highly derived movements found in Apidae, the evolution of the corbicula with its corbicular scopa presumably preceded that of the highly derived behavior and associated structures (rastellum, penicillum) used in pollen packing. This suggestion is supported by the structure of certain African Meliponinae, as described below.

The progenitors of the Meliponinae would not have had such specialized meliponine features as reduced wing venation and stings, but might well have had the ancestral apid pollen-carrying apparatus. There exist in Africa today groups of meliponines in which the corbicula is fully developed, but in which the tibio-tarsal region lacks (primitively or by loss?) one or both of the special structures that relate to corbicular packing in other Meliponinae. Groups which lack the rastellum are *Trigona* subgenera *Meliplebeia, Axestotrigona,* and *Hypotrigona* as well as the genus *Meliponula.* Of these taxa the subgenus *Hypotrigona* has only a weakly developed penicillus which could not function as described in the section on Ipsilateral Type II Pollen Packing. In the other groups listed the penicillum bristles are not so nicely graded in length and curviture as illustrated and described in that section; the penicillum in such cases may well serve only or primarily to support the pollen mass. These same groups have the largest (and flattened) sting sheaths of any Meliponinae; this must be an ancestral feature and thus strengthens the hypothesis that at least in some cases the lack of rastellum and perhaps the weak penicillum are primitive features rather than losses. (These morphological data, but not the interpretations, are from Dr. A. Wille, *in litt.*) Pollen packing in these African groups has not been studied, but it seems almost certain that in *Hypotrigona,* at least, it is like the packing of nest materials and Type I pollen packing described above, i.e., eutypical; the middle legs presumably place sticky pollen directly into the corbiculae. The American subgenus *Trigonisca,* a relative of the African *Hypotrigona,* has relatively feeble penicilla and rastella, and its pollen packing, so far as known, is like that postulated for the ancestral groups, although it may also have in its repertoire the derived pollen-packing methods of most Meliponinae.

Pollen Packing in the Apidae. Eutypical pollen manipulation as seen in Apidae in-

volves synchronous movements of the legs of a given pair. Thus the two middle legs even in a *Trigonisca* resting on a petal simultaneously place pollen on the ipsilateral corbiculae. In this respect apids differ from at least many of the non-apid bees, which transfer pollen back to the tibial scopa by movement of one leg at a time. (Observations of non-apids in flight are still needed; their leg movements may then be synchronous.) Movement of both middle and hind legs appears to facilitate pollen transfer to the corbicula, making it easier to get the mid basitarsus to the proper position relative to the hind leg. Simultaneous movement of both mid and hind legs is difficult, however, while the bee uses at least one of these pairs of legs for support. Most apids solve this problem by hovering when employing derived (Type II) pollen-packing methods, so that the legs are freed for the pollen-transferring movements. Such behavior has seemingly been transmitted to males of the Euglossini which use similar movements for transferring scents to the hind tibiae while hovering. Presumably a behavioral pattern that evolved among females was activated in males, which in any case must carry the appropriate genes for it.

Within the Meliponinae, several derived features of pollen manipulation have arisen. Like most Apoidea, meliponines commonly collect pollen with the front tarsi, as well as on other parts of the body when the pollen is loose. Many and perhaps all species of *Trigona* are unusual among bees in that they transfer the pollen from the forelegs onto the thoracic venter and leg bases for temporary storage. It is later picked up by the middle legs (or possibly again by the front legs). We suspect that *Melipona* has lost this behavior for we find no special accumulations of pollen on the mesepisterna and coxae in this genus, nor are there coarse hairs in these areas like those of *Trigona*. *Melipona* workers move so rapidly that details of their pollen manipulation have eluded us. (Our attempts at observation were mostly made at flowers of *Mimosa*, where the *Melipona* rushes around through the stamens, all parts of its hairy body being dusted with pollen.)

In the species of *Trigona* that we have studied most thoroughly, pollen is transferred to the corbicula by drawing the pollen-bearing middle tarsus across the apex of the ipsilateral hind tibia and base of the basitarsus in such a way that the pollen appears to be picked up and pushed basad onto the corbicula by a structure found only in this subfamily, the penicillum. This behavior resembles eutypical movements in that pollen is transferred to the hind leg by the ipsilateral middle leg, but is derived in that it is not placed directly into the corbicula. In the course of this movement pollen will also be scraped off of the mid basitarsus by hairs of the auricular area of the ipsilateral hind basitarsus.

Pollen also appears to be transferred from inner sides of hind basitarsi to contralateral corbiculae in meliponines. They scrape pollen from the abdomen with the hind basitarsi. Meliponines with a penicillum ordinarily also have a row of bristles across the inner side of the apex of the tibia, the rastellum, which can comb the inner side of the contralateral basitarsus. When large amounts of pollen are combed off of a basitarsus by a rastellum, the pollen accumulates outside the rastellum and can be pushed basad, onto the corbicula, by basitarsal movements which are effective because of the direction of the hairs of the auricular area and perhaps because of the pollen already on those hairs. However, for most meliponines it is probably more important that such pollen can presumably stick to and be carried basad by other pollen transferred to the hind leg by the ipsilateral middle leg.

For many of the commonest species of *Trigona,* the importance of the inner side of the hind basitarsus in transferring pollen seems reduced. In the subgenus *Trigona s. str.* which includes the species that we have studied most carefully and in many species of the subgenus *Tetragona,* there is a large, hairless, sericeous area occupying up to half of the inner basitarsal surface. Accumulations of pollen on this surface have not been seen and are not common even among the hairs on the rest of the surface. These groups are placed among the derived subgenera of *Trigona.* Their rather hairless abdomens and perhaps the nature of the flowers usually visited by them may make brushing of the abdomen of little importance. Probably contralateral pollen transfer is more important in other subgenera in which the under surface of the hind basitarsus is fully covered with bristles of stiff hairs.

Finally for Meliponinae, the gleaning bees of the subgenus *Scaura* represent a noteworthy development, with a concave auricular area or false auricle in the swollen hind basitarsus for pushing pollen upward onto the corbicula. The broad basitarsi as well as the abdominal hairs are used to brush up pollen from flower and leaf surfaces.

In the remaining Apidae (Apinae and the tribes Bombini and Euglossini of the Bombinae) pollen manipulation is also of derived types, but partially different from those of Meliponinae. In the Apinae and Bombini, whose hind tibial and tarsal structure is very similar, pollen from the inner surface of the hind basitarsus is combed off by the contralateral rastellum; it sticks to the tibial apex outside the rastellum, and is then pushed upward onto the corbicula by the strongly developed auricle.

In the Euglossini there is also an auricle although it appears small because of the enormously expanded hind tibia. The auricle is closely appressed to the swelling or bulla of the tibial apex, so that pollen from the contralateral basitarsus presumably could not be pushed between these leg segments onto the auricle, as in *Apis* and *Bombus.* Moreover, the rastellum does not project mesally in such a way that it could easily comb the contralateral basitarsal hairs, as it does in the other three apid groups. Pollen must therefore be placed on the outside of the hind leg by the middle leg, presumably in the area of the tibiotarsal joint; then it is probably pushed basad into the huge corbicula by the auricle and other basal marginal parts of the basitarsus which slide over the tibial bulla as the basitarsus moves.

If Winston and Michener (1977) have correctly presented the cladistic relationships among apid groups, the Euglossinae must have lost the contralateral pollen transfer and the relatively large auricle characteristic of *Bombus* and *Apis.* The great enlargement of the tibia associated with carrying huge loads of nesting materials and pollen may have had this effect by narrowing the space between the auricle and the swollen tibial apex. Alternatively, the Euglossinae might be, in features of pollen manipulation (as well as in solitary or parasocial behavior), primitive Apidae that, like certain African Meliponinae, have never evolved contralateral pollen transfer. Many more observations of pollen-collecting Euglossinae are needed to settle this problem.

DERIVATION OF POLLEN MANIPULATION FROM SELF-GROOMING MOVEMENTS. Pollen transfer from the foreleg to the middle leg is indistinguishable from the corresponding cleaning movement (Jander, 1976) and is therefore considered homologous to it. The middle leg, with the pollen on its under and inner side, swings backward in eutypical pollen transfer towards the ipsilateral hind leg. The pollen on the middle leg is then pressed into the scopa, and simultaneously the middle leg is pulled

forward and basad relative to the hind tibia, so that the distad-directed hairs of the scopa scrape the pollen off the middle leg. This final scopal loading movement is precisely the opposite of, and presumably derived from, normal self-cleaning behavior, during which bees typically remove dust from the outer side of the hind leg with a distad scraping movement of the ipsilateral middle leg. This cleaning movement, however, is used inside the nest for scraping the collected pollen out of the scopa. (Our remarks above ignore the femoral, trochanteral, coxal, propodeal, and sternal scopal areas of many colletids, halictids, and andrenids, partly for lack of data, but also because in the context of the Apidae it is the tibial scopa that is important.)

Patting of the corbicular pollen load with the middle basitarsus, presumably to adjust and shape the pollen mass, is seen in most or all apids. This movement differs from normal cleaning of the outside of the hind leg and probably from Type I pollen packing movements mainly by suppression of scraping and rubbing components. It is likely that patting is derived from eutypical or Type I pollen-packing movements, which are themselves probably derived from normal cleaning movements. The movements of the mid legs in ipsilateral Type II pollen packing presumably have the same origin.

The derived pollen-manipulating movements of the Apidae also mostly appear to have evolved from cleaning movements. Bees typically clean one middle leg at a time by scraping off foreign particles usually with both but sometimes with only one hind basitarsus. The middle leg is pulled forward, usually between the two hind basitarsi, while the hind legs are pushed backward and downward (Beeken, 1934; Farish, 1972). It is by this very movement that the pollen is transferred from the middle leg to the inner side of the hind basitarsus by Bombini and Apinae and at least some Meliponinae.

After a bee has cleaned its middle legs between the hind basitarsi, it regularly cleans the latter by pressing them flat against each other and then rubbing them with alternating longitudinal pumping movements. During these movements the tarsi are in continuous contact. Dirt is thereby pushed distad because all bristles and hairs on the inner sides of the hind basitarsi point in that direction. [This cleaning movement was observed in all of the 60 species of bees in seven families listed by Jander (1976) and differs from the corresponding cleaning movement of most other Hymenoptera which clean the hind basitarsus by pulling it past the tibiotarsal joint of the contralateral hind leg (Farish, 1972; Wagner, 1959). Normally terminal tibial spurs improve the efficiency of this movement and the so-called strigil of the hind leg of sphecids is its morphological concomitant.] In the pollen manipulation of Meliponinae, Bombini and Apinae an almost typical apoid movement pattern is used when pollen is combed off of the inner surface of the hind basitarsus by the contralateral tibial comb or rastellum. The only known difference between this pollen manipulation and the true cleaning movement is that during the latter the tarsi are pressed against each other while during the former the tarsi are slightly bent apart so that only the distad-moving rastellum contacts the contralateral hind basitarsus. For the final auricular movement that pushes pollen basad from the rastellum into the corbicula, no homologous self-cleaning movement is known.

The peculiar temporary storage of pollen on the thoracic venter and coxae in the genus *Trigona* appears to be the reverse of a widespread cleaning movement in which the forelegs scrape backward on the underside of the thorax, as has been observed in *Nomada vincta, Ceratina* (*dupla* or *calcarata*), *Bombus ruderatus* and *Psithyrus variabilis* (R.J.). Further transfer of pollen could easily be mediated by the

middle legs, since backward scraping of the coxae by the middle legs as a component of self cleaning has been seen in *Triepeolus concavus, Anthophora abrupta,* and *Trigona jaty* (R.J.) and has been described for *Apis mellifera* by Beeken (1934).

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THE UNIVERSITY OF KANSAS
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UNIVERSITY

SUMMER CRANE FLIES OF LAKE ITASCA VICINITY, MINNESOTA

By
George W. Byers

Vol. 51, No. 20, pp. 603-613 March 9, 1979

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THE UNIVERSITY OF KANSAS
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Vol. 51, No. 20, pp. 603-613 March 9, 1979

Summer Crane Flies of Lake Itasca Vicinity, Minnesota[1]

George W. Byers

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ABSTRACT

Eighty species of Tipulidae and three of Ptychopteridae are recorded for a limited area near the forest-prairie border of north-central Minnesota. The collections were made during five weeks of June and July, 1970. Species new to the region include *Ctenophora apicata, Limnophila bryanti, Hexatoma cinerea, Ormosia megacera* and *Molophilus novacaesariensis*. Ecological, seasonal and geographical distribution of each species are summarized.

To this basic list are added 12 species of the Lake Itasca area from the collection of the University of Minnesota, of which *Limnophila similis* is a new regional record.

[1] Contribution No. 1691 from the Department of Entomology, University of Kansas, Lawrence Kansas, 66045. This study was supported in part by grant DEB-77-15868 from the National Science Foundation, which concerns mainly the genus *Nephrotoma*. Technical assistance by Mr. Chen-Wen Young is acknowledged with thanks.

INTRODUCTION

Following is a record of crane flies (Tipulidae) and phantom crane flies (Ptychopteridae) collected in the vicinity of Lake Itasca, Clearwater County, Minnesota, between 19 June and 20 July 1970. During this period, 22 collections were made on 19 different days and the major habitats were sampled repeatedly. This was not a concentrated field study, but was incidental to the teaching of a five-week course in general entomology. Nevertheless, the list of species is judged to be fairly representative of the early summer season. Addition of the species of spring and late summer should increase the known regional fauna of these flies considerably.

Lake Itasca, source of the Mississippi River, at 454 m (1475 ft) above sea level, is surrounded by a patchy intermingling of hardwood forest and coniferous forest. The hardwoods, entering the region from the southeast, include oaks, some maple, ash and others. The eastern coniferous forest includes jack pine, red pine and white pine, largely characteristic of areas to the east, and some balsam fir and spruce more representative of the subarctic forests. Paper-bark birch is scattered through both these forest types. Wide expanses of aspen cover areas once deforested by logging operations or burning. Annual precipitation in the region is only about 57 cm (23 inches), but water is abundantly evident in virtually all habitats. Lakes and ponds are numerous and are fed by and often interconnected by slowly moving streams. Intervening land includes wooded swamps, acidic *Sphagnum* bogs and marshy meadows. Black spruce and tamarack occur in boggy environments, and alder and willow shrubs are common along the streams. Open marshy areas, often adjoining the many small lakes in the region, are characterized by the presence of sedges and grasses. Forest undergrowth comprises a profusion of herbaceous plant species, mosses, ferns and lycopods.

Although the forest is more or less continuous eastward to the Atlantic Ocean, southeastward to the Gulf of Mexico, and northward to Hudson Bay, it ends almost abruptly about 65 km (40 mi) west of Lake Itasca, giving way to open prairie on the bed of Pleistocene Lake Agassiz. Many of the forest crane flies found here are, accordingly, near the westernmost edge of their range; some others, truly boreal, range on to the northwestward in the subarctic forest, north of the plains.

The collections include about equal numbers of species of the subfamilies Tipulinae (39 species in 4 genera, 22 of these in the large genus *Tipula*) and Limoniinae (40 species in 16 genera) and a single species in the Cylindrotominae, as well as three species of Ptychopteridae. Many of these are boreal species that range broadly across Canada and southward in and near the Appalachian Mountains. Virtually all are species with extensive ranges in eastern North America, especially in northeastern United States and southeastern Canada. A few are reported from the region for the first time, having been recorded earlier from no further west than Michigan (Rogers, 1942) or even farther to the east.

Dickinson's "The Crane Flies of Wisconsin" (1932) is the only extensive faunal study of Tipulidae made anywhere near the Lake Itasca region. It lists 130 species and one subspecies of tipulids and one ptychopterid. It should be useful in giving some idea of the species to be expected in the Lake Itasca area but not found by me in this study. Rogers (1942) found 201 species of crane flies and two of Ptychopteridae in an area of southeastern Michigan that is in many ways ecologically similar to the Lake Itasca region. Nearly 400 species are known from the entire state of Michigan (my unpublished list); the number in Wisconsin and Minnesota is surely near 300.

Since this list of 95 species is clearly incomplete for the region, I have omitted taxonomic keys, illustrations and other aids to identification. Taxonomic keys and illustrations may be found in Alexander's (1942) paper on the Tipulidae of Connecticut (in which the keys cover the fauna of temperate and boreal eastern North America) and in Dickinson's paper.

Species are recorded in the sequence in which they appear in the Catalog of the Diptera of America North of Mexico (Stone et al., 1965). In most instances the names are those given in the Catalog; some subgeneric assignments in *Tipula* have been changed to conform to more recently published taxonomic views, and occasionally the catalogued subspecies are rejected for the reasons stated in my comments.

Following the name of each species and that of its author is a subjective estimate of its abundance in the Lake Itasca area from 19 June to 20 July 1970:

rare—only one individual collected, or only a few all at one place and on one date,

uncommon—a few specimens taken, at two or three different places or dates,

occasional—several specimens taken, but at only 2-4 places or on widely scattered dates,

numerous—species present in such numbers that, in favorable habitats, 10-20 individuals could be collected in an hour,

common—present in most habitats and in such numbers that in the more favorable places 20-50 individuals could be netted in an hour of collecting,

abundant—of such numbers that in the more favorable habitats 50 or more specimens could be collected in an hour, and usually present in most habitats.

Seasonal occurrence is indicated by actual dates of collection or spans of dates.

Previously recorded range (abbreviated PR) is indicated by naming the northeasternmost state or province in which the species has been found, then the northwesternmost, followed by names of states indicating the southern boundary of the range, generally from west to east. State and provincial names are usually abbreviated.

ANNOTATED LIST OF SPECIES

Tipulidae

Ctenophora (Ctenophora) apicata Osten Sacken. Rare; one female of the dark-winged form found resting on a slightly decayed aspen log (a likely larval habitat) in mixed forest near a swamp, on 4 July. One female, somewhat less melanic, from Ponemah Point, Red Lake, Beltrami Co., 3 July. PR—N.Y., New England and s.e. Canada, 1600 km (1000 mi) or more to the east; these specimens thus constitute a new regional record.

Ctenophora (Tanyptera) dorsalis Walker. See appendix.

Nephrotoma alterna (Walker). Occasional in dense, low herbaceous vegetation at forest borders. 24 June, 3 and 14 July. Recorded as *N. incurva* Loew in older literature. Typical form reported earlier from N.S. w. to Mich. and s. to Fla.; subspecies *nexilis* Dietz recorded from Colo., Man., Minn. and Wis. The Lake Itasca specimens are somewhat paler overall than those from more eastern and southern localities but do not have the color markings used by Dietz to differentiate *nexilis*.

Nephrotoma breviorcornis (Doane). Rare; one male and one female taken in low streamside vegetation, 15 July. PR—Que. w. to Wis., s. to Iowa and S.C.

Nephrotoma ferruginea (Fabricius). Occasional, especially in open, grassy areas near buildings but also in upland woods; larvae usually in sod. 27 June-5 July. Species widespread in eastern North America and Rocky Mountain region; PR—Nfld. w. to Alta., s. to Colo., N. Mex. and Ga.

Nephrotoma gracilicornis (Loew). Rare or uncommon in low vegetation near swamp and lake margins. 3 and 13 July. A subspecies *temeraria* (Dietz) has been recorded from northern Michigan and Wisconsin, but I consider this a synonym of the typical form. PR—N.Y. and Ont. w. to Wis., s. to Pa. and Md.

Nephrotoma lugens (Loew). Uncommon; in shaded tall grasses along lake shore. 20-25 June. PR—N.S. w. to Minn., s. to Ill. and N.C.

Nephrotoma macrocera (Say). Occasional in dense herb-shrub vegetation at edge of swamp. Only females were collected. 27 June-19 July. PR—Maine w. to Wis., s. to Kans., Tenn. and Fla.

Nephrotoma occipitalis (Loew). Uncommon; from dense growth at swamp margin to

drier woods of birch and aspen with ground cover of grasses and broad-leaved herbs. 20-27 June. PR—a boreal species from northern Canada, N.B. n.w. to N.W.T., s. to Colo. and Mich.

Nephrotoma sodalis (Loew). Uncommon in grassy areas of the park. 17 June and 2 July. PR—Que. to Wis., s. to N.C.

Nephrotoma tenuis (Loew). Uncommonly taken in herbaceous vegetation, both along swamp margins and in upland woods. 13-19 July. PR—Maine w. to Wis., s. to Tenn. and N.C.

Dolichopeza (Dolichopeza) americana Needham. Uncommon; taken in deeply shaded niche below a boulder projecting from a bank at trailside, together with *D. obscura* and *D. tridenticulata*. 24-27 June. PR—widespread from Labr. n.w. to Alaska, s. to Alta., S.D., Ill. and n. Ga.

Dolichopeza (Oropeza) dorsalis (Johnson). Fairly common in herbaceous vegetation in open swampy woods and along margins of swamps. 4-15 July. PR—N.S. w. to n. B.C., s. to S.D., N.C. and n. Fla. Variation in length of the petiole (vein M_{1+2} beyond m) of cell M_1 is common locally, from distinctly petiolate (more than half as long as vein M_1) to obliterated, with cell M_1 sessile on cell 1st M_2 (cf. Byers 1961:809-810).

Dolichopeza (Oropeza) obscura (Johnson). Numerous; taken from time to time in low vegetation at swamp margin, but more often found resting in a group in deep shade below an outcropping boulder at trailside, together with *D. americana* and *D. tridenticulata*. 1-19 July. PR—N.S. w. to Alta., s. to Ark. and Fla.

Dolichopeza (Oropeza) similis (Johnson). Occasionally taken from shaded cranny beneath fallen log about 30 m from swamp but more often around upturned roots of fallen trees in swamp, or in shade of dense vegetation over muddy spots or low, mossy hummocks in swamp. 24 June-1 July. PR—Maine w. to Man., s. to s. Mich. and w. Md.

Dolichopeza (Oropeza) tridenticulata Alexander. Uncommonly collected, but in concentrations of several flies; all specimens taken from shaded niche below boulder projecting from a bank. See *D. obscura*. 27 June-4 July. PR—Maine, Que. w. to Man., s. to Mo. and Ga.

Dolichopeza (Oropeza) venosa (Johnson). Uncommon; taken together with *D. similis* in shade of upturned roots of fallen trees in swamp, or elsewhere in deeply shaded parts of swamp and nearby woods. 24 June-1 July. PR—Nfld. w. to Yukon, s. to Wis., Ohio and N.J.

Dolichopeza (Oropeza) walleyi (Alexander). Occasional; generally distributed in low herbaceous stratum of woods, both near swampy areas and in upland woods, but never commonly collected. 27 June-15 July. PR—N.S. w. to Alta., s. to S.D., Mo. and Fla.

Tipula (Schummelia) hermannia Alexander. Occasional in shaded, low vegetation of streamside and swamp border habitats. 30 June-13 July. PR—Nfld. w. to Wis., s. to Kans. and Fla.

Tipula (Nippotipula) abdominalis (Say). Several larvae collected from shallow, detritus-filled concavities at shore of Mississippi River near its source, on 30 June. PR—Nfld. w. to Wis., s. to Kans. and n. Fla.

Tipula (Yamatotipula) caloptera Loew. Uncommon in grasses 20-70 cm high in shade of alder shrubs and birch and aspen trees along the Mississippi River near its source at the north end of Lake Itasca. In wing coloration, these flies resemble *T. (Y.) noveboracensis* Alexander, and the median lobe of the ninth abdominal tergum of the males is not an evenly rounded and blackened structure (as in typical *caloptera*) but a broad, almost truncated lobe with a small median point. 16-20 July. PR—Nfld. w. to Wis., s. to Mo. and Fla.

Tipula (Yamatotipula) sulphurea Doane. Rare; only one female taken in deep shade of luxuriant herbaceous foliage in a wooded swamp, together with *Dolichopeza similis*. 1 July. PR—Maine w. to Mich. (but an apparently isolated subspecies recorded from Wyoming), s. to Ind.

Tipula (Yamatotipula) tephrocephala Loew. Occasional; among ferns, *Carex* and broad-leaved herbs at the margin of a swamp, also in similar habitat by the lake shore. 20 June-1 July. PR—Nfld. w. to Wis., s. to Ind. and Pa.

Tipula (Yamatotipula) tricolor Fabricius. Occasionally found in grass-sedge habitats, often in only partial shade, both at the headwaters of the Mississippi River (north end of Lake Itasca) and in a low swale beside Mary Lake (south of the east arm of Lake Itasca). A preponderance of males during the few days the species was seen suggests a single mid-summer generation. 10 and 16-20 July. PR—Maine and Que. w. to Wis., s. to Ark. and Fla.

Tipula (Yamatotipula) vicina Dietz. Rare; a single male taken among sedges beneath willow and alder shrubs along the Mississippi River about 9 km north of its source. 30 June. PR—Nfld. w. to Mich., s. to Pa.

Tipula (Angarotipula) illustris Doane. Uncommonly collected, but locally numerous in low, leafy vegetation of swamps or in grassy marshes and swales. 10-19 July. Recorded as *Prionocera* (or *Stygeropis*) *fuscipennis* Loew in older literature. PR—Nfld. w. to B.C., s. to Idaho, Colo., Ohio and N.J.

Tipula (Vestiplex) canadensis Loew. Rare; one male taken in low, leafy plants on hillside above swamp. 27 June. PR—Labr. n.w. to N.W.T., s. to Alta. and Ont.

Tipula (Pterelachisus) angulata Loew. Common in low herbaceous stratum of upland woods, also in lower swales among orchids, wild ginger, *Equisetum,* etc.; uncommon in vegetation at swamp border. 19 June-13 July. In several males, the tip of vein R_{1+2} is atrophied (and in one specimen it is absent in one wing, present in the other), cell 1st M_2 is about as long as cell M_1, and the median "tooth" in the notch of the ninth abdominal tergum is indistinct or lacking. Thus, these males would run to *Tipula subfasciata* Loew in existing keys. If the two nominal species prove to be synonymous, *subfasciata* is the older name. PR—N.S. w. to Wis., s. to Ill., Tenn. and N.C.

Tipula (Pterelachisus) entomophthorae Alexander. Rare; only one female taken in partially shaded ferns, grasses and sedges at headwaters of Mississippi River, north end of Lake Itasca, on 16 July. PR—Labr. and Nfld. w. to Alta., s. to Ind. and N.C.

Tipula (Pterelachisus) illinoiensis Alexander. Rare; one female found among bracken ferns, *Equisetum* and herbaceous plants in woods near swamp margin. 20 June. PR—N.H. w. to Man., s. to Ill.

Tipula (Pterelachisus) penobscot Alexander. Rare; only one female taken among ferns and *Equisetum* at the edge of a swamp, on 1 July. PR—N.B. w. to Alta., s. to Mich. and Pa.

Tipula (Pterelachisus) senega Alexander. Uncommon; in low, leafy vegetation on wooded hillside above swamp (forest about 60% spruce and pine, 40% aspen and birch). 24-27 June. PR—Nfld. w. to Alta., s. to Iowa and N.J.

Tipula (Pterelachisus) serta Loew. See appendix.

Tipula (Pterelachisus) trivittata Say. Occasional; lakeside woods, once in swale with orchids, horsetail *(Equisetum),* wild ginger, etc., but usually in more upland woods among aspens, birches, spruce and pine. 20 June-13 July. PR—Nfld. w. to Iowa, s. to Kans., Tenn. and S.C. (with a subspecies recorded from Wyoming).

Tipula (Beringotipula) borealis Walker. Rare; one male, the prey of a lestid damselfly, taken in deep grass beneath birches and aspens, near the Mississippi River near its source, on 20 July. PR—N.S. w. to Wis., s. to Kans. and S.C.

Tipula (Beringotipula) helderbergensis Alexander. Occasional in swamp-margin vegetation, particularly in bracken and other ferns, *Equisetum, Aralia* and other low plants. 27 June-13 July. PR—N.B. w. to Mich., s. to N.Y.

Tipula (Beringotipula) latipennis Loew. One

of the commonest crane flies in the early-summer fauna. Common to abundant in the shaded grasses, ferns and leafy herbaceous plants (30 cm to 1 m high) of swamp borders, on hillsides and in upland woods, in both evergreen and mixed forest habitats; less common in forest ecotones near open areas. 24 June-20 July. PR—N.S. w. to Alta., s. to Wis., s. Mich. and N.J.

Tipula (Beringotipula) resurgens Walker. Uncommon; in low plants of swamp borders, especially among ferns and *Equisetum*. 1-13 July. PR—Nfld. w. to Alta., s. to Ind. and Md. Recorded in older literature as *Tipula grata* Loew.

Tipula (Lunatipula) dorsimacula Walker. See appendix.

Tipula (Lunatipula) duplex Walker. See appendix.

Tipula (Lunatipula) megaura Doane. Rarely collected; two males and a female in deep grasses at edge of scrubby second-growth woods. 14 July. PR—Que. w. to Minn., s. to Iowa and Vt.

Tipula (Lunatipula) parshleyi Alexander. Occasional; in grasses and herbs 40-60 cm high in flat, wooded area near swamp; also in deep grasses at edge of low, second-growth woods. 19 June and 11-14 July. PR—Nfld. w. to Alta., s. to Colo., s. Mich. and Mass.

Tipula (Lunatipula) valida Loew. See appendix.

Tipula (Lunatipula) youngi Alexander. Fairly common in ferns, *Aralia* and other vegetation of upland woods and slopes above swampy areas. Collected in ratio of 13 males to 1 female, yet over many days, suggesting the females are somehow elusive (i.e., that this was not a sampling of the early part of the emergence period). 24 June-15 July. PR—Nfld. n.w. to Alaska, s. to Alta., Wis. and N.Y.

Liogma nodicornis (Osten Sacken). Adults occasionally found locally in herbaceous vegetation and lower branches of trees in mixed forest; larvae occur in mosses such as *Mnium* found where adults were taken. 19-27 June. PR—Nfld. w. to Alta., s. to Ill. and Va.

Limonia (Limonia) tristigma (Osten Sacken). A mid-summer species taken only near the end of the period of this report, therefore rated as uncommon although it is generally an abundant, widespread species; collected from ferns near a swamp border, also from deep grass beneath birches and aspens. 19-20 July. PR—N.B. w. to Alta., s. to Ill. and N.C.

Limonia (Metalimnobia) cinctipes (Say). Uncommon; collected from deep shade beneath a boulder projecting from a bank, where it was resting together with *Dolichopeza* spp. 1 July. Two males and two females identified as this species, but smaller than usual and with atypical wing markings, were found on 27 June and 1, 15 and 19 July. Size variation in *L. cinctipes* is well known. This species is sometimes regarded as a North American race of the palearctic *Limonia annulus* (Meigen). PR—Nfld. w. to Alta., s. to Mo., Miss. and Fla.

Limonia (Metalimnobia) fallax (Johnson). Occasionally collected from shaded grasses, ferns, *Aralia, Equisetum, Aster,* etc., at edges of swamps and lakes. 20 and 27 June, 10 and 20 July. PR—N.J. w. to Mich., s. to Okla. and N.C.

Limonia (Metalimnobia) solitaria (Osten Sacken). Abundant in nearly all shaded habitats, particularly in luxuriant vegetation bordering swamps, but also spreading into the more upland woods; the commonest, most ubiquitous tipulid encountered in the region, taken throughout the period of this report. Not found in streamside vegetation along the Mississippi River in any of the collections made there. 19 June-19 July. PR—N.S. n.w. to Alaska, s. to Minn. and Mass.

Limonia (Metalimnobia) triocellata (Osten Sacken). Rare; only one male collected from shaded ferns and *Carex* at the edge of a swamp. 19 July. PR—N.S. w. to Alta., s. to Kans., Ill., Tenn. and Ga.

Limonia (Discobola) annulata (Linnaeus). Rare; a single male taken in herbaceous growth 30-70 cm high in low, flat woods

near the edge of a swamp. 11 July. PR—Nfld. w. to B.C., s. to Ore., Iowa, Tenn. and Va.; also widespread in Eurasia.

Limonia (Rhipidia) fidelis (Osten Sacken). Rare; a single female collected in low plants on slope above a swamp. 4 July. PR—N.S. w. to Alta., s. to Ore., Ill., Tenn. and Fla.

Limonia (Rhipidia) lecontei Alexander. See appendix.

Limonia (Dicranomyia) brevivena (Osten Sacken). See appendix.

Limonia (Dicranomyia) haeretica (Osten Sacken). Rare; one female found in luxuriant broad-leaved plants at the margin of a swamp, on 13 July. PR—Nfld. w. to Mich., s. to N.Y.

Limonia (Dicranomyia) immodesta (Osten Sacken). Numerous; taken at several localities in both the swamp-margin habitat and further up the slopes into the upland woods. 29 June-19 July. PR—N.S. w. to Alta., s. to Iowa and S.C.

Limonia (Dicranomyia) immodestoides Alexander. See appendix.

Limonia (Dicranomyia) liberta (Osten Sacken). See appendix.

Limonia (Dicranomyia) morioides (Osten Sacken). Rare; only one male found among ferns and horsetails *(Equisetum)* at the margin of a swamp. 27 June. PR—Nfld. n.w. to Alaska, s. to Colo., Mo. and N.C.

Limonia (Geranomyia) communis (Osten Sacken). Occasionally swept from deeply shaded lakeside and streamside grasses and from swamp borders. 25 June-16 July. PR—Nfld. w. to B.C., s. to Calif., La. and Fla. Note: this species has often been confused with *L. canadensis* (Westwood); the flies recorded here would key to *canadensis* in most current keys, e.g., that in Alexander, 1942.

Helius (Helius) flavipes (Macquart). Uncommon; in luxuriant broad-leaved vegetation at the edge of a swamp and spreading into drier woods on nearby slopes. 27 June-4 July. PR—N.S. w. to Alta., s. to Tex. and Fla.

Pedicia (Pedicia) albivitta Walker. Rare; only two individuals taken, both in vegetation 70-90 cm high, in deep shade near small streams, at two localities but both on 21 June. PR—Nfld. w. to Man., s. to Mo. and S.C.

Pedicia (Tricyphona) inconstans (Osten Sacken). Rare during this collection period although usually a common species in most parts of its range; only one male taken about 50 cm above ground in deep grass beside the Mississippi River approximately 350 m north of its source. 20 July. PR—Nfld. w. to Minn., s. to Mo. and Ga.

Epiphragma (Epiphragma) fasciapennis (Say). Common, particularly in the more upland woods, on broad-leaved herbaceous plants 60-90 cm high (a habitat shared with *Limonia solitaria* and *Pilaria* spp.). 19 June-4 July. PR—Nfld. w. to Alta., s. to La. and Fla.

Austrolimnophila (Austrolimnophila) toxoneura (Osten Sacken). Occasional; in dense, low vegetation along swamp margins. 24 June-13 July. PR—Nfld. w. to Wis., s. to Tenn. and Va.

Pseudolimnophila (Pseudolimnophila) inornata (Osten Sacken). Common to abundant in nearly every shaded habitat, but especially near water. Although the larvae are aquatic, the adults freely move up the slopes into the upland woods. 19 June-15 July. PR—Nfld. w. to Wis., s. to Ind. and Md.

Pseudolimnophila (Pseudolimnophila) noveboracensis (Alexander). Abundant and taken in more separate collections than *P. inornata,* particularly near water but also spreading up the slopes to upland woods. 1-19 July. PR—N.S. w. to B.C., s. to Utah and S.C.

Limnophila (Phylidorea) adusta Osten Sacken. Uncommon; in woods near pond, in one instance, and in the *Carex*-filled bed of a dried forest pond in another. 29 June and 14 July. PR—Nfld. w. to Wis., s. to Ill. and N.C.

Limnophila (Phylidorea) platyphallus Alexander. Rare; only one male taken in shaded vegetation 30-60 cm high, at swamp margin on 16 July. PR—N.S.

w. to Alta., s. to Mich. and Pa.

Limnophila (Phylidorea) similis Alexander. See appendix.

Limnophila bryanti Alexander. Rare; a single female taken by sweeping sedges under sparse woods of aspen and birch beside the Mississippi River where it is about 5 m wide, clear, with sand and boulder bottom. 30 June. PR—reported earlier only from Alberta.

Limnophila poetica Osten Sacken. Rare; only two males, both from dense undergrowth of wooded swamps. 27 June and 9 July. PR—Que. n.w. to Alaska, s. to B.C., Ill. and Mass.

Shannonomyia lenta (Osten Sacken). Occasional; in ferns and sedges at margins of swamps and in similar vegetation beside a small stream. 9-19 July. PR—Nfld. w. to Ill., s. to Tenn. and Ga., with a subspecies recorded from the Gaspé region of Quebec.

Pilaria meridiana (Staeger). See appendix.

Pilaria recondita (Osten Sacken). Abundant, especially on low, broad-leaved plants, in nearly every habitat and throughout the collecting period; absent only from all three collections made along the banks of the Mississippi River and one lakeshore collection (cf. *Limonia solitaria*). 19 June-19 July. PR—N.S. w. to Minn., s. to La. and Fla.

Pilaria tennipes (Say). Uncommon; taken in leafy vegetation of a swamp margin on 1 July and in shaded, deep grass by the Mississippi River on 20 July. PR—N.B. w. to Wis., s. to Kans., Tex. and Fla.

Hexatoma (Eriocera) cinerea (Alexander). Rare; only two males taken in sedges in the shade of alder bushes at the edge of the Mississippi River about 13 km north of its source, on 30 June. PR—Que. w. to Ont., s. in mountains to e. Tenn. and S.C. This collection represents a westward extension of the range of some 1000 km (625-650 mi).

Gnophomyia (Gnophomyia) tristissima Osten Sacken. Numerous in shaded, leafy vegetation up to about 1 m high in swamp borders and more upland woods, also in sparse birch-aspen woods along the Mississippi River. 27 June-19 July. PR—Que. and Maine n.w. to N.W.T., s. to Tex. and Fla.

Gonomyia (Idiocera) blanda Osten Sacken. See appendix.

Gonomyia (Gonomyia) subcinerea Osten Sacken. Occasional, but possibly overlooked in some habitats; taken only along border of one swamp and on adjacent slopes, but on various dates from 24 June to 19 July. In general a common, widespread species. PR—Nfld. w. to B.C., s. to Wash., Utah, Kans. and Fla.

Cheilotrichia (Empeda) stigmatica (Osten Sacken). Rare; taken only once (a male), in the swamp-margin habitat, on 27 June. PR—Nfld. w. to S.D., s. to Tenn. and N.C.

Erioptera (Symplecta) cana (Walker). Rare in this series of collections, although this is one of the commonest tipulids in North America. Only one female found in hillside vegetation in forest of spruce, pine, birch and aspen. 27 June. Since this species is one of the first on the wing in spring, the first generation was probably waning by mid-June. PR—Nfld. w. to B.C. and throughout the U.S.

Erioptera (Erioptera) chlorophylla Osten Sacken. Occasional in leafy herbs of swamp margins and up adjacent slopes a short distance; also in shaded, swampy areas at the edges of lakes; appeared earlier in the season than the very similar *E. chlorophylloides*. 4-19 July. PR—N.S. w. to Wis., s. to Tenn. and Fla.

Erioptera (Erioptera) chlorophylloides Alexander. Occasional and generally in the same habitats as the preceding species, but also found in ferns and sedges at the source of the Mississippi River. 15-19 July. PR—Nfld. w. to Colo., s. to Tenn.

Erioptera (Erioptera) septemtrionis Osten Sacken. Rare; only two males and a female taken at light in western Hubbard County, near the eastern edge of Itasca State Park, on 7 July. PR—Nfld. w. to Wash., s. to Calif., Kans. and Fla.

Erioptera (Erioptera) villosa Osten Sacken. Numerous; taken among ferns, sedges

and leafy herbaceous plants of swamp borders and swampy areas at edges of lakes and ponds, but occasionally spreading up wooded slopes; found once in streamside sedges. 9-16 July. PR—Nfld. w. to Sask., s. to Utah, Colo. and N.Y.

Erioptera (Mesocyphona) caliptera Say. Like the preceding species, a generally common species, but rare in this locality during this particular season. Found in dense, leafy vegetation of a swamp border. 13 July. PR—Nfld. w. to Calif., s. into Centr. and S. Amer. and Fla. Recorded as *E. caloptera* in older literature.

Ormosia (Ormosia) manicata (Doane). Rare; one male found in luxuriant vegetation 50-70 cm high along the margin of a swamp. 4 July. PR—Nfld. w. to Wash., s. to Calif. and Pa.

Ormosia (Ormosia) megacera Alexander. Rare; two males collected from rank herbaceous growth at swamp margin. 13 July. PR—Que. and Nfld. s.w. to Pa. This is accordingly a new regional record, the nearest previous localities being approximately 1600 km (1000 mi) to the east.

Ormosia (Ormosia) monticola (Osten Sacken). Common in both low wooded areas such as swamp margins and stream banks and in upland woods, associated with low, leafy plants and deep grasses. 19 June-19 July. PR—N.B. w. to Mich., s. to N.C.

Molophilus (Molophilus) hirtipennis (Osten Sacken). Uncommon in shaded swamp-margin vegetation. 13-19 July. PR—Nfld. w. to Ont., s.w. to Ill., Tenn. and N.C.

Molophilus (Molophilus) novacaesariensis Alexander. Rare; one female only, identified (with some doubt) as this species by its wing venation and small size; from low vegetation of swamp border; found together with *M. hirtipennis*. 13 July. PR—N.J. w. to Ind., s. to Fla.; if this specimen is correctly identified it represents a new regional record.

Ptychopteridae

Ptychoptera metallica Walker. Numerous; among grasses and broad-leaved herbs in unshaded lakeside seepage habitat with saturated sandy but humous soil; less often in grass-sedge microhabitats in swampy woods. 20 June-19 July. PR—widely scattered records from Ont., Minn., Alta. and Colo.

Ptychoptera quadrifasciata Say. Common in two localities, both grass-sedge habitats, one partially shaded, near the Mississippi River's source, the other in an unshaded swale near a smaller stream. 10-16 July. PR—Que. w. to Ill., s. to Fla. This species was recorded as *Ptychoptera rufocincta* Osten Sacken in much of the older literature.

Bittacomorpha clavipes (Fabricius). Common in grass-sedge habitats at edges of streams and lakes and around hillside seepage areas, also in rank herbaceous growth of swamp margins, usually in shade, but often in full sunlight. 25 June-19 July. PR—Nfld. w. to Man., s.w. to Ariz. and s. to Tex. and Fla.

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Appendix

After the above was in press, a collection of crane flies from the Lake Itasca region became available from the University of Minnesota, through the cooperation of Dr. Edwin F. Cook. This collection, spanning the years 1914 to 1964, includes 12 species that I did not find. Some of these species have a flight season that normally ends before mid-June; others were taken in early summer but for some reason I overlooked them during the weeks of my own collecting. Many were collected in light traps, a method I did not use. With one exception, the University of Minnesota specimens are not accompanied by habitat data. In some instances the dates of collection add to those recorded above.

Names of the twelve additional species have been inserted at the appropriate places in the basic list, but details concerning them appear below. For most other species in the University of Minnesota collection, only the dates of collection (for all years together) are given.

Ctenophora (Ctenophora) apicata. 9 and 16 July.

Ctenophora (Tanyptera) dorsalis Walker. Rare; one male, two females, all of the *topazina* form with yellowish wings. 25 June and 17 July. PR—Nfld. w. to Wis., s. to Ill., Ohio and N.C.

Nephrotoma alterna. 10 July.

Nephrotoma brevicornis. 3 July.

Nephrotoma ferruginea. 16 June-15 July, 21 Aug.

Nephrotoma gracilicornis. 17 June-9 July, at light.

Nephrotoma lugens. 14-30 June, 13 July, 17 Aug.

Dolichopeza (Oropeza) walleyi. 17 July.

Tipula (Nippotipula) abdominalis. 1 Aug. (cf. larval record above).

Tipula (Yamatotipula) sulphurea. 17-29 June, 14 Aug.

Tipula (Yamatotipula) tephrocephala. 14 June-1 July.

Tipula (Yamatotipula) tricolor. 12-15 July.

Tipula (Angarotipula) illustris. 5 and 15 July.

Tipula (Pterelachisus) angulata. 16 June, 4 July.

Tipula (Pterelachisus) entomophthorae. 28 May.

Tipula (Pterelachisus) senega. 25 June.

Tipula (Pterelachisus) serta Loew. Probably occasional; 29 May, 9 June-13 July. PR—Labr. w. to Alta., s. to Minn., Mich. and N.Y.

Tipula (Pterelachisus) trivittata. 11-18 June.

Tipula (Beringotipula) helderbergensis. 18 June, 14 July.

Tipula (Beringotipula) latipennis. 17 June, 10-15 July.

Tipula (Beringotipula) resurgens. 24 June, 7-29 July.

Tipula (Lunatipula) megaura Alexander. 12 July.

Tipula (Lunatipula) dorsimacula Walker. Probably numerous in late spring; 22 May-14 June. PR—N.S. w. to B.C., s. to Calif., Colo., Kans. and N.J.

Tipula (Lunatipula) duplex Walker. Rare; a single female, taken on 9 July. PR—N.S. w. to Mich., sw. to Kans. and s. to Tenn. and n. Fla.

Tipula (Lunatipula) parshleyi. 14 June-8 July.

Tipula (Lunatipula) valida Loew. Rare; a single male, taken 17 June. PR—Nfld. w. to Minn., s. to Ill. and N.C.

Tipula (Lunatipula) youngi. 18 and 29 June.

Limonia (Metalimnobia) cinctipes. 27 July. One female reared from the fungus *Polyporus dryophilus;* this is a small, atypically marked individual, as described above under *L. cinctipes.*

Limonia (Metalimnobia) solitaria. 25 June.

Limonia (Metalimnobia) triocellata. 28 July.

Limonia (Rhipidia) lecontei Alexander. Rare; one female, taken at light trap, 2 July. PR—Nfld. nw. to Alaska, s. to Calif., Kans. and Va. In much of the older literature, this species has been identified as *L. (Rh.) maculata* Meigen.

Limonia (Dicranomyia) brevivena (Osten Sacken). Four females taken at light, all on 9 July. PR—Nfld. w. to Ore., s. to Fla.

Limonia (Dicranomyia) haeretica. 9 July.

Limonia (Dicranomyia) immodestoides Alexander. Probably locally common; 23 individuals, all females and all taken at light. 14-17 June, 2-9 July. PR—Nfld. w. to Ore., s. to Kans. and Ind.

Limonia (Dicranomyia) liberta (Osten Sacken). This species should be common in the Lake Itasca region; however, I did not find it, and the University of Minnesota collection contains only one male, one female, from light trap, 27 June. PR—Nfld. w. to Man., s. to Okla. and Fla.

Limonia (Geranomyia) communis. 13 June, 2 July, 2 and 10 Aug.

Helius (Helius) flavipes. 5 July, at light.

Epiphragma (Epiphragma) fasciapennis. 25 June.

Pseudolimnophila (Pseudolimnophila) inornata. 14 June-11 July.

Pseudolimnophila (Pseudolimnophila) noveboracensis. 10 Aug.

Limnophila (Phylidorea) similis Alexander. Rare; one male, one female identified as this species but with some doubt. The gonapophyses are as shown for *similis* by Alexander (1942: 399, fig. I), but the aedeagus is about as long as the gonapophyses, its two apophyses not divergent but approximately paralleling the aedeagus; outer dististyle nearest that of *L. fratria* O.S. PR—Que., Ont., N.Y. and Mass. The range is thus extended westward by 1000 km (625 mi) or more.

* These two references not cited in text but used as sources of locality data.

Shannonomyia lenta. 21 June.

Pilaria meridiana (Staeger). One female, 7 July. PR—Maine w. to Ore., s. to Colo.; also in Eurasia. This species has often been recorded as *P. osborni* Alexander.

Pilaria recondita. 13-21 July.

Gnophomyia (Gnophomyia) tristissima. 13 June, in light trap.

Gonomyia (Idiocera) blanda Osten Sacken. Apparently numerous locally; five males, 12 females taken at light, 5 and 19 July. PR—N.S. w. to Alta., s. to Mo. and Fla.

Gonomyia (Gonomyia) subcinerea. 9 July, at light.

Erioptera (Symplecta) cana. 28 May, 14-24 June, 2-10 July.

Erioptera (Erioptera) chlorophylloides. 11 July (one male); eight females of the *chlorophylla* group, 2-8 July, could belong to this species or to *chlorophylla.*

Erioptera (Erioptera) septemtrionis. 5-14 June, most taken at light.

Erioptera (Erioptera) villosa. 6-8 July, at light.

Erioptera (Mesocyphona) caliptera. 21 June.

Molophilus (Molophilus) hirtipennis. 30 June.

Ptychoptera metallica. 11 Aug.

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PROTOZOA FROM ACID-BOG MOSSES AND FOREST MOSSES OF THE LAKE ITASCA REGION (MINNESOTA, USA)

By
Eugene C. Bovee

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The *University of Kansas Science Bulletin* (continuation of the *Kansas University Quarterly*) is an outlet for scholarly scientific investigations carried out at the University of Kansas or by University faculty and students. Since its inception, volumes of the *Bulletin* have been variously issued as single bound volumes, as two or three multi-paper parts or as series of individual papers. Issuance is at irregular intervals, with each volume prior to volume 50 approximately 1000 pages in length. Effective with volume 50, page size has been enlarged, reducing the length of each volume to about 750 pages.

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Protozoa from Acid-bog Mosses and Forest Mosses of the Lake Itasca Region (Minnesota, USA)

Eugene C. Bovee[1]

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ABSTRACT

In a comparison of protozoa associated with mosses from an acid sphagnum bog of the Lake Itasca (Minnesota, USA) region with those associated with forest mosses there, these were found: Among bog mosses 145 protozoa were identified to genus, 96 of those to species; 33 were Mastigophora from 2 subphyla, 6 classes, 7 orders, 10 families and 21 genera; 56 were Sarcodina, from 2 subphyla, 3 classes, 4 orders, 13 families and 23 genera; 56 were Ciliophora, from 3 subphyla, 8 classes, 16 orders, 29 families and 37 genera. Among forest mosses 68 protozoa were identified to genus, 46 of those to species; 9 were Mastigophora from 2 subphyla, 3 classes, 3 orders, 4 families and 7 genera; 39 were Sarcodina from 2 subphyla, 3 classes, 7 orders, 12 families and 23 genera; 30 were Ciliophora from 3 subphyla, 7 classes, 12 orders, 21 families and 24 genera. 23 protozoa characteristically restricted to bog mosses were found in the bog, 8 being testate sarcodines, 15 being ciliates. 33 protozoa characteristically associated with forest soils or forest mosses were found with the forest mosses, 17 being testate sarcodines, 16 being ciliates. Two different associations exist in the two habitats. Only one sarcodine was characteristically found in both habitats. The ciliates of the two associations, though often of the same or similar genera, were more often different species, except for certain cosmopolitan ones.

INTRODUCTION

Lake Itasca, a large spring-fed lake in Clearwater County, Minnesota, USA, is the source of the Mississippi River. It is surrounded by a Pleistocene-glaciated terrain, supporting a mixed hardwood and coniferous forest of red, jack and white pine, ash, maple, oak and other hardwoods, aspen and birch. Other lakes and ponds, with interconnecting meandering streams, are numerous in the region, with intervening wooded swamps, acidic bogs and marshy meadows. Black spruce and tamarack occur near the bogs,

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and willow and alder along the streams. Open marshes adjoin many of the smaller lakes, supporting abundant growth of sedges and grasses. Forest undergrowth includes many herbaceous plants, mosses, ferns and lichens.

The region, with its varied habitats and many microenvironments, presents much opportunity for studying ecological interrelationships of the numerous organisms that occur in them.

One group of organisms, the Protozoa, have largely been ignored in the ecology of the region. Even though rainfall is not heavy (~57cm/annum), water is abundant in the glacially tilled terrain, the air is humid and the habitats moist. Hence, it is an excellent area for studies of protozoan ecology.

This paper presents the results of a short, intensive study of protozoa found associated with mosses of bogs compared to those found with forest mosses in the region. Many observers have reported protozoa among mosses, especially bog mosses and forest mosses, e.g., Penard (1902, 1905, 1909, 1922), Hoogenraad and DeGroot (1952), Heal (1961), Štěpánek (1963) and others. Some protozoa, especially certain ciliates deemed characteristically associated with mosses, have been so named as to reflect that association, e.g., *Balantidiopsis muscicola, Condylostoma sphagni, Glaucoma sphagni, Phacodinium muscorum, Spirostomum sphagni, Vorticella muralis,* and others (Penard, 1922).

Other researchers, working with dried mosses from herbaria, have noted that different species of mosses may harbor different spectra of protozoa, especially of testate amebas. (Hoogenraad and DeGroot, 1952; Štěpánek, 1963). Heal (1961) found that associations of testate amebas in bog mosses differed from those of fen mosses in England, the species of *Sphagnum* mosses also differing in bogs *versus* fens. Bonnet and Thomas (1960) found that associations of testate amebas in soils or on mosses differ with the nature of the soil and species of mosses in the eastern Pyrenees Mountains. Stout (1963) found that protozoan associations of ciliates, naked and testate amebas in forest soils and litters differ in samples from mor, calcareous mull, or acid mull substrates from England's Chiltern Hills.

All of these observers found some protozoan species to be cosmopolitan, but others restricted more-or-less closely to specific microhabitats related to one or more of several ecological parameters. Those parameters include the kind(s) of mosses, the type(s) of soil, the pH (acid or alkaline) of the soil, the type and quality of humus, the types of plants on the soil, the specific soil horizon, and the relative moistness and drainage of the soil.

This study of the protozoa associated with bog mosses (*Sphagnum* spp.) compared to those of forest mosses of the Lake Itasca region of Minnesota indicates differences worth noting and worth further study. A listing of the protozoa found is given.

MATERIALS AND METHODS

Two samples of *Sphagnum* spp. and water around them were collected during early August, 1977, from the Buell Bog[2] immediately adjoining (on the south) Highway 113 (Minnesota), 1¼ mi W of the SE entry to the Lake Itasca State Park, latitude N 47° 7′ 45″ and longitude W 95° 11′, altitude ~1600 ft. These samples were kept in moist (glass) chambers in a laboratory at 18°-22°C. Another sample of mosses was taken from a rotten, fallen log near the "Ice-House Pond" on the grounds of the Biological Station in the Park, latitude N 47° 13′ 13″ and latitude W 95° 11′, altitude ~1590 ft. It contained mainly the mosses *Brachythecium salesdrosum, Mnium cuspidatum* and *Pylaisiella selwynii*.[3] These were likewise kept in a moist chamber.

About 0.2 ml of water and detritus squeezed from a moss was placed on a clean, glass microscope-slide, then covered with a #1 coverglass sealed in place peripherally with petroleum jelly. The protozoa on the slide were observed at 40, 100, and 430× magnifications by phase-contrast lighting. Such a slide could be observed during 48 hrs or more to notice live protozoa thereon and identify them.

Two to 8 such slides were prepared each day and were examined, a total of 70 slides being observed to identify protozoa present, 38 from the bog-moss samples and 32 from the forest moss sample.

A list of protozoa seen in the samples was recorded, keying each one to genus and, when possi-

[2] Named after the late Dr. Murray Buell, algologist, who taught algology many summer sessions at the Lake Itasca Biology Station, often using this bog as a field laboratory and teaching site.

[3] Dr. Frank Bowers, Biology Department, Wisconsin State University, Stephens Point, Wisconsin, kindly identified these mosses for me.

ble, to species, using a variety of monographic books and papers (Allegre and Jahn, 1943; Corliss, 1977; Jahn and Jahn, 1949; Johnson, 1944; Kahl, 1935; Kudo, 1966; Penard, 1902, 1905, 1909, 1922; Shawhan and Jahn, 1947; and others). Particular attention was given to the ciliates and testate sarcodines, since they are the Protozoa more often recorded previously as being characteristic of mossy habitats.

The Protozoa are classified herein according to the scheme of Jahn, Bovee and Jahn (1979).

RESULTS

In the *Sphagnum* spp. from the Buell Bog, 145 species of Protozoa were identified to genus, 97 of those to species. Others seen too briefly to be identified are not included. Of the identified organisms 33 were of the Phylum Mastigophora (29 Phytomastigophora, 4 Zoomastigophora) of 2 subphyla, 6 classes, 7 orders, 10 families and 21 genera. Those of the Phylum Sarcodina totalled 56 species identified to genus, 42 of those to species, from 2 subphyla, 3 classes, 4 orders, 13 families and 23 genera. The Phylum Ciliophora was represented by 56 kinds identified to genus, 37 of them to species, from 3 subphyla, 8 classes, 16 orders, 29 families and 37 genera. No protozoa of the Phylum Sporozoa were found among the *Sphagnum* mosses of the Buell Bog samples.

In the forest mosses there were 68 species of Protozoa identified to the genus, 52 of them to species. Of the Subphylum Mastigophora 2 subphyla, 3 classes, 3 orders, 4 families, 7 genera and 9 species were represented. The Subphylum Sarcodina had 2 subphyla, 3 classes, 7 orders, 12 families, 23 genera and 39 species represented. The Subphylum Ciliophora was represented by 3 subphyla, 7 classes, 12 orders, 21 families, 24 genera and 30 species. No members of the Phylum Sporozoa were found in the forest moss samples.

In the Buell Bog mosses, as well as the many more or less cosmopolitan protozoa seen, there were a number of protozoa listed by other authors as found mainly on or restricted to mosses, especially on *Sphagnum* spp. These were: 1. Sarcodines (Filida); *Assulina seminulum, Euglypha cristata, Trinema penardi.* Sarcodines (Lobeda); *Arcella artocrea, Nebela collaris, Heleopora picta, Hyalosphenia papilio, Hyalosphenia elegans.* 2. Ciliates; *Drepanomonas dentata; Litonotus muscororum; Bryophyllum sphagni; Spathidium amphoriforme; Prorodon cinereus; Leptopharynx sphagnetorum; Holophyra saginata; Colpoda steini; Frontonia depressa; Cylidium elongatum; Cyclidium muscicola; Vorticella lichenicola; Keronopsis helluo; Euplotes muscicola; Blepharisma sphagni.*

In the forest mosses, similarly, there were a number of Protozoa identified by others as primarily associated with forest mosses, forest soils and the rhizospheres of forest plants. Those include: 1. Sarcodines (Filida); *Euglypha ciliata; E. ciliata* form *glabra; E. umbilicata; E. laevis; Trinema penardi; Corythion dubium; C. pulchellum; Assulina muscororum; Difflugiella oviformis; Cryptodifflugia compressa.* Sarcodines (Lobeda); *Centropyxis sylvatica, C. s.* form *minor; C. platystoma; C. elongata; Cyclopyxis puteus; C. kahli; C. ambigua.* 2. Ciliates; *Spathidium muscicola; S. spatula; S. amphoriforme; Colpoda cucullus, C. inflata, C. irregularis, C. penardi; Tillina magna; Nassula protectissima; Microthorax simulans; Pseudoglaucoma muscorum; Cyclidium muscicola; C. terricola; Gonostomum affine; Gastrostyla muscororum; Rhabdostyla muscorum.*

It is noteworthy that only *one* species characteristic of the sphagnum bog was also found in the forest mosses and is considered characteristic of both, namely, *Assulina seminulum.* Bonnet and Thomas (1960) also found it to be cosmopolitan in their soil and moss samples.

Table I shows the Protozoa that were found in the Buell Bog. Table II shows the Protozoa found in the forest mosses.

DISCUSSION

In comparing the protozoan populations of the bog mosses to those of forest mosses, it is clear, as might be expected, that the more edaphic species occur with the forest mosses. The species associated with bog mosses tend to be aquatic and acidophilous, or cosmopolitan species. The edaphic nature of the forest moss associates is indicated, among ciliates, by (usually) the presence of smaller species with reduced surface area. Plates I

TABLE I.

PROTOZOA ASSOCIATED WITH *Sphagnum* MOSSES OF BUELL BOG.

- Phylum MASTIGOPHORA
  - Subphylum PHYTOMASTIGOPHORA
    - Class CRYPTOMONADEA
      - Order Cryptomonadida
        - Family Cryptomonadidae
          - *Chilomonas paramecium*
          - *Cryptomonas* sp.
    - Class CHRYSOMONADEA
      - Order Chromulinida
        - Family Chromulinidae
          - *Chrysococcus* sp. #1
          - *Chrysococcus* sp. #2
          - *Chrysococcus* sp. #3
        - Family Anthophysidae
          - *Cephalothamnion* sp.
    - Class VOLVOCEA
      - Order Volvocida
        - Family Volvocidae
          - *Pandorina morum*
          - *Eudorina elegans*
          - *Polytoma* sp.
    - Class EUGLENEA
      - Order Euglenida
        - Family Euglenidae
          - *Euglena klebsi*
          - *Euglena proxima*
          - *Euglena terricola*
          - *Astasia longa*
          - *Astasia klebsi*
          - *Astasia* sp. #3
          - *Astasia* sp. #4
          - *Phacus pyrum*
          - *Rhabdomonas* sp.
          - *Menoidium incurvum*
          - *Menoidium acutissima*
        - Family Trachelomonadidae
          - *Trachelomonas verrucosa*
      - Order Peranemida
        - Family Peranemidae
          - *Peranema trichophorum*
          - *Distigma proteus*
        - Family Petalomonadidae
          - *Petalomonas trisulcatum*
          - *Petalomonas* sp. #2
        - Family Anisonemidae
          - *Anisonema acinus*
          - *Anisonema* sp. #2
          - *Entosiphon sulcatum*
          - *Entosiphon* sp. #2
  - Subphylum ZOOMASTIGOPHORA
    - Class PROTOMASTIGIA
      - Order Choanomastigida
        - Family Codosigidae
          - *Codosiga* sp.
      - Order Bodonida
        - Family Bodonidae
          - *Bodo* sp.
          - *Colponema loxodes*
    - Class KARYOMASTIGEA
      - Order Dikaryomastigida
        - Family Hexamitidae
          - *Hexamita* sp.
- Phylum SARCODINA
  - Subphylum AUTOTRACTA
    - Class ACTINOPODEA
      - Order Heliozoida
        - Family Acanthocystidae
          - *Acanthocystis* sp.
          - *Pinaciophora* sp.
    - Class FILORETICULOSEA
      - Order Filida
        - Family Euglyphidae
          - *Assulina seminulum*
          - *Euglypha cristata*
          - *Euglypha laevis*
          - *Euglypha tuberculata*
          - *Euglypha umbilicata*
          - *Paraeuglypha* sp.
          - *Pseudoeuglypha gracilis*
          - *Tracheleuglypha dentata*
          - *Trinema lineare*
          - *Trinema penardi*
          - *Trinema complanatum*
          - *Trinema* sp. #4
  - Subphylum HYDRAULA
    - Class CYCLEA
      - Superorder Lobeda
        - Order Granulopodida
          - Family Arcellidae
            - *Arcella artocrea*
            - *Arcella catinus*
            - *Arcella discoides*
            - *Arcella hemisphaerica*
            - *Arcella mitra*
            - *Arcella vulgaris*
          - Family Centropyxidae
            - *Centropyxis aculeata*
            - *Centropyxis* sp. #2
            - *Cyclopyxis arcelloides*
          - Family Cryptodifflugiidae
            - *Cryptodifflugia oviformis*
          - Family Difflugiidae
            - *Difflugia avellana*
            - *Difflugia bidens*
            - *Difflugia elegans*
            - *Difflugia fallax*
            - *Difflugia globulosa*
            - *Difflugia lebes*
            - *Difflugia oblonga*
            - *Difflugia olla*
            - *Difflugia pyriformis*
            - *Difflugia viscidula*
            - *Difflugia* sp. #11
            - *Difflugia* sp. #12
            - *Lesquereusia spiralis*

TABLE I. (Continued.)

- Family Plagiopyxidae
  - *Plagiopyxis callida*
- Family Hyalospheniidae
  - *Hyalosphenia elegans*
  - *Hyalosphenia papilio*
- Family Nebelidae
  - *Heleopora picta*
  - *Nebela bursaria*
  - *Nebela collaris*
  - *Nebela tubercnlata*
  - *Nebela* sp. #4
- Family Quadrulellidae
  - *Paraquadrula discoides*
- Order Pelobiontida
- Family Pelomyxidae
  - *Pelomyxa palustris*
  - *Pelomyxa belevskii*
- Order Eruptida
- Family Hartmannellidae
  - *Saccamoeba lucens*
  - *Saccamoeba* sp. #2
- Order Conopodida
- Family Mayorellidae
  - *Mayorella* sp. #1
  - *Mayorella* sp. #2
  - *Mayorella* sp. #3
- Order Pharopodida
- Family Vannellidae
  - *Vannella minor*
  - *Vannella* sp. #2
- Incertae sedis
  - *Mastigamoeba* sp.

Phylum CILIOPHORA

Subphylum KINETOFRAGMINOPHORA

Class HYPOSTOMEA

- Order Nassulida
- Family Nassulidae
  - *Nassula* sp. #1
  - *Nassula* sp. #2
- Family Microthoracidae
  - *Drepanomonas dentata*
- Family Leptopharyngidae
  - *Leptopharyx sphagnetorum*
- Order Cyrtophorida
- Family Chilodonellidae
  - *Chiodonella cucullulus*
- Family Chlamydodontidae
  - *Chlamydodon* sp.

Class GYMNOSTOMEA

- Order Pleurostomatida
- Family Amphileptidae
  - *Amphileptus claparedei*
  - *Amphileptus* sp. #2
  - *Bryophyllum sphagni*
  - *Litonotus muscororum*
  - *Loxophyllum* sp.
- Order Karyorelictida
- Family Loxodidae
  - *Loxodes magnus*
  - *Loxodes* sp. #2
- Order Haptorida
- Family Enchelyidae
  - *Lacrymaria* sp.
- Family Spathidiidae
  - *Spathidium amphoriforme*
- Family Trachelidae
  - *Dileptus anser*
  - *Dileptus cygnus*
- Order Prorodontida
- Family Prorodontidae
  - *Prorodon discolor*
  - *Prorodon cinereus*
- Family Colepidae
  - *Coleps bicuspis*
  - *Coleps inermis*
  - *Coleps octospinus*
  - *Coleps* sp. #4
- Order Prostomatida
- Family Holophryidae
  - *Holophrya saginata*

Class VESTIBULIFEREA

- Order Colpodida
- Family Colpodidae
  - *Colpoda steini*

Subphylum OLIGOHYMENOPHORA

Class HYMENOSTOMEA

- Order Hymenostomatida
- Family Glaucomidae
  - *Monochilum frontatum*
- Family Frontoniidae
  - *Frontonia depressa*
- Family Lembadionidae
  - *Lembadion bullinum*
- Order Scuticociliatida
- Family Uronematidae
  - *Uronema* sp.
- Family Loxocephalidae
  - *Loxocephalus plagius*
- Family Cyclidiidae
  - *Cyclidium elongatum*
  - *Cyclidium muscicola*

Class PERITRICHEA

- Order Sessalida
- Family Vorticellidae
  - *Vorticella campanula*
  - *Vorticella picta*
  - *Vorticella lichenicola*
  - *Vorticella* sp. #4

Subphylum POLYHYMENOPHORA

Class HETEROTRICHEA

- Order Stichotrichida
- Family Holostichidae
  - *Holosticha vernalis*
  - *Holosticha* sp. #2
  - *Keronopsis helluo*
  - *Uroleptis limnetis*
  - *Uroleptis* sp. #2
- Family Keronidae
  - *Kerona rubra*

TABLE I. (Continued.)

Order Sporadotrichida
Family Oxytrichidae
Onychodromus grandis
Stylonychia sp.
Family Euplotidae
Euplotes muscicola
Euplotes sp. #2
Class SPIROTRICHEA
Order Heterotrichida
Family Spirostomidae
Blepharisma sphagni
Blepharisma sp. #2
Spirostomum minus
Spirostomum teres
Family Metopidae
Metopus intercedens
Metopus sp. #2
Metopus sp. #3
Family Bursariidae
Bursaria truncatella
Bursaria sp. #2
Class OLIGOTRICHEA
Order Oligotrichida
Family Halteriidae
Halteria grandinella

TABLE II.

PROTOZOA ASSOCIATED WITH FOREST MOSSES.

Phylum MASTIGOPHORA
Subphylum PHYTOMASTIGOPHORA
Class VOLVOCEA
Order Chlamydomonadida
Chlamydomonas sp.
Class EUGLENEA
Order Euglenida
Family Euglenidae
Rhabdomonas sp.
Order Peranemida
Family Anisonemidae
Anisonema sp.
Family Petalomonadidae
Petalomonas mediocanellata
Petalomonas sp. #2
Subphylum ZOOMASTIGOPHORA
Class PROTOMASTIGEA
Order Bodonida
Family Bodonidae
Bodo sp. #1
Bodo sp. #2
Cercobodo sp.
Rhynchomonas nasutum
Phylum SARCODINA
Subphylum AUTOTRACTA
Class ACTINOPODEA
Order Heliozoida
Family Ciliophryidae
Ciliophrys sp.
Class FILORETICULOSEA
Order Filida
Family Euglyphidae
Assulina muscororum
Corythion dubium
Corythion pulchellum
Euglypha ciliata
Euglypha ciliata form *glabra*
Euglypha cristata
Euglypha laevis
Euglypha strigosa
Euglypha umbilicata
Euglypha vanoyei
Placocista spinosa
Trinema penardi
Family Difflugiellidae
Cryptodifflugia compressa
Difflugiella minuta
Difflugiella oviformis
Subphylum HYDRAULA
Class CYCLEA
Superorder Lobeda
Order Granulopodida
Family Amoebidae
Amoeba proteoides
Family Centropyxidae
Centropyxis elongata
Centropyxis platystoma
Centropyxis silvatica
Centropyxis silvatica form *minor*
Cyclopyxis ambigua
Cyclopyxis kahli
Cyclopyxis puteus
Family Difflugiidae
Cucurbitella sp.
Lesquereusia modesta
Pontigulasia bigibbosa
Order Eruptida
Family Vahlkampfiidae
Vahlkampfia sp.
Family Hartmannellidae
Saccamoeba sp. #1
Saccamoeba sp. #2
Saccamoeba sp. #3
Order Conopodida
Family Mayorellidae
Mayorella sp. #1
Order Pharopodida
Family Vannellidae
Platyamoeba sp. #1
Vannella sp. #1
Vannella sp. #2

TABLE II. (Continued.)

- Order Thecida
  - Family Thecamoebidae
    - *Thecamoeba granifera*
    - *Thecamoeba* sp. #2
  - Family Striamoebidae
    - *Striamoeba bradys*
    - *Striamoeba quadrilineata*
- Phylum CILIOPHORA
  - Subphylum KINETOFRAGMINOPHORA
    - Class GYMNOSTOMEA
      - Order Haptorida
        - Family Spathidiidae
          - *Spathidium amphoriforme*
          - *Spathidium muscicola*
          - *Spathidium spatula*
        - Family Trachelliidae
          - *Dileptus gracilis*
        - Family Actinobolinidae
          - *Actinobolina vorax*
      - Order Pleurostomatida
        - Family Amphileptidae
          - *Amphileptus* sp.
    - Class VESTIBULIFEREA
      - Order Trichostomatida
        - Family Plagiopylidae
          - *Plagiopyla* sp.
      - Order Colpodida
        - Family Colpodidae
          - *Colpoda cucullus*
          - *Colpoda inflata*
          - *Colpoda irregularis*
          - *Colpoda penardi*
          - *Tillina magna*
    - Class HYPOSTOMEA
      - Order Nassulida
        - Family Nassulidae
          - *Nassula protectissima*
        - Family Leptopharyngidae
          - *Leptopharynx* sp.
        - Family Microthoracidae
          - *Microthorax simulans*
      - Order Cyrtophorida
        - Family Chilodonellidae
          - *Chilodonella wisconsinensis*
    - Class SUCTORIA
      - Order Exogenida
        - Family Podophryidae
          - *Podophyra collini*
  - Subphylum OLIGOHYMENOPHORA
    - Class HYMENOSTOMEA
      - Order Hymenostomatida
        - Family Tetrahymenidae
          - *Colpidium* sp.
        - Family Glaucomidae
          - *Monochilum* sp.
          - *Pseudoglaucoma muscorum*
      - Order Scuticociliatida
        - Family Cinetochilidae
          - *Cinetochilum margaritaceum*
        - Family Cyclidiidae
          - *Cyclidium muscicola*
          - *Cyclidium terricola*
    - Class PERITRICHEA
      - Order Sessalida
        - Family Epistylididae
          - *Rhabdostyla muscorum*
  - Subphylum POLYPHYMENOPHORA
    - Class HETEROTRICHEA
      - Order Stichotrichida
        - Family Holostichidae
          - *Gonostomum affine*
          - *Keronopsis* sp.
        - Family Keronidae
          - *Kerona* sp.
      - Order Sporadotrichida
        - Family Oxytrichidae
          - *Gastrostyla muscorum*
        - Family Aspidiscidae
          - *Aspidisca* sp.
    - Class OLIGOTRICHEA
      - Order Oligotrichida
        - Family Halteriidae
          - *Halteria grandinella*

& II shows the comparative size and morphological contours of forest moss ciliates versus bog moss or cosmopolitan species. Plates III, IV & V show characteristic testate amebas from the two associations.

Among the sarcodines that form shells, again the forest-moss-associated species are the more edaphic. The numerous aquatic species of *Arcella, Hyalosphenia, Nebela* and *Difflugia* associated with the bog mosses are replaced by species of *Centropyxis, Cyclopyxis* and *Difflugiella* on the forest mosses. *Trinema lineare,* and *Corythion dubium* of the bog-mosses are replaced on forest mosses by *T. penardi* and *C. pulchellum.* Although *Euglypha cristata* and *E. laevis* are found in both associations, they are less numerous on the forest mosses, which also harbor *E. ciliata, E. umbilicata, E. vanoyei* and *E. strigosa,* species that were not present on bog mosses.

Among the flagellates found in the two associations, phytoflagellates were found only among the bog mosses (except for a lone *Chlamydomonas* sp. in the forest mosses sample). Even for the bog mosses the phytoflagellates were limited to a few, generally cosmopolitan species. Colorless flagellates

were largely euglenoids in the bog moss association, but with both euglenoids and bodonids in the forest moss association.

For other groups, comparisons are difficult to make without further study and will not be attempted until further data can be obtained.

Even so, it is evident that the two types of moss-associations are much different so far as the Protozoa they support, the bog-moss Protozoa being largely acidophilous and aquatic, the forest-moss-associated Protozoa being the more edaphic.

A comparison of the Protozoa of the Lake Itasca forest mosses to those found by Stout (1963) from soil and litter of the Chiltern Hills shows little similarity for testate sarcodines, except the presence of cosmopolitan *Assulina seminulum, Trinema lineare, Euglypha laevis* and *E. ciliata*. Some ciliates noted by Stout (loc. cit.) were found either in our bog moss or forest moss samples, but with no distinct relationship to either association.

There is, however, a distinct resemblance of the testate sarcodines found in the Lake Itasca forest moss sample to those reported by Bonnet and Thomas (1960) from soils and mosses of the eastern Pyrenees Mountains. They list *Euglypha ciliata* and *E. c.* form *glabra, Trinema lineare* and *Difflugiella oviformis* as characteristic of forest mosses. Those were also present in the Lake Itasca forest moss sample. They found *Corythion dubium, Euglypha laevis, Centropyxis silvatica, Cyclopyxis puteus, C. kahli,* and *C. arcelloides* to be cosmopolitan in the forest. The Lake Itasca forest moss sample contained all but *C. arcelloides*. That was found on the bog mosses.

Although our earlier brief study (Sanford and Bovee, 1974) suggests the probability that some protozoans (e.g., certain species of testate amebas) are more often associated with one moss than another, no attempt was made in this study to determine such a relationship.

However, Hoogenraad and DeGroot (1952) noted distributional differences of testate amebas on 5 species of *Sphagnum* collected in New Jersey. Only *Assulina muscorum, A. seminulum* and *Trinema lineare* were found on all 5 species. For the genus *Difflugia,* they found that no species thereof was to be found on more than 3 of the 5 *Sphagnum* spp. *Amphitrema* spp. were seen on only 2 of the *Sphagnum* spp., the other Lobeda being each limited to a single species of *Sphagnum*. *Hyalosphenia* spp. were present on only 2 of the 5 *Sphagnum* spp. They also noted distributional differences for *Nebela* spp., *Centropyxis* spp. and *Euglypha* spp. on the 5 species of *Sphagnum* from New Jersey.

Sanford and Bovee (loc. cit.), examining bog mosses from Twin Lakes near Lake Itasca, compared the testate amebas found on *Sphagnum* spp. to those on other genera of mosses from the same bog. They found *Hyalosphenia papilio, Heleopora petricola, Arcella hemisphaerica, Quadrulella symmetrica, Cryptodifflugia oviformis, Assulina seminulum* and *Euglypha cristata* only on *Sphagnum* spp. They noted *Euglypha ciliata, E. filifera, Arcella costata, A. dentata* and *Centropyxis aculeata* on other mosses, but *not* on *Sphagnum* spp. Some amebas were on both groups of mosses, but more often on *Sphagnum* spp., e.g., *Euglypha alveolata,* or conversely more prevalent on other mosses than on *Sphagnum* spp., e.g., *Euglypha laevis, Trinema lineare, Arcella vulgaris,* or were about equally distributed, e.g., *Difflugia globulosa* and *Difflugia binucleata.*

Bamforth (1969) in examining the moist, generally-acid forest litters and underlying soils in Louisiana for Protozoa, found that certain testate amebas predominated in litters, others in the moist soils. In the litters he found *Centropyxis* spp. common, but they were infrequent in soils. In this study I found *Centropyxis* spp. more numerous in the forest mosses than in the bog-mosses. Bamforth (loc. cit.) also remarked that the testate amebas found in his study were generally those of *Sphagnum* bog habitats. Of 19 species from 10 genera that he found, I found in Buell Bog 7 of the 10 genera, but only 8 of the 19 species that he found, and 4 of those are generally considered to be probably cosmopolitan. Evidently, while the genera are similar, there is a likely differential

distribution of species due to some of the ecologic factors cited earlier in this paper.

Chardez (1957, 1960, 1965, 1967, and other papers) and with Krizelj (1970) has extensively catalogued the protozoan fauna (especially testacid amebas) of forest soils and of mosses (from sphagnum bogs, of forest floors, rocks and tree trunks). He finds (1967), as I have found, that the different habitats—bogs, moist forest floor, soils, or mosses above ground—exhibit distinct faunas of protozoa, larger species being found in bogs, progressively smaller ones in the less to more dry situations.

He (1967) considers *Arcella* spp. typical of lakes and ponds, *Difflugia* spp. characteristically found among aquatic mosses, with species differing with the locale and species of mosses, *Cyclopyxis* spp. typical of mosses above ground (as I have found, also), differing species of *Centropyxis* in different situations (*Centropyxis aculeata* in wet locales and *C. platystoma* in drier ones).

Some species he finds (1957) generally distributed on forest mosses, e.g., *Corythion dubium, Assulina muscorum, Trinema lineare* (I found all three on forest mosses). Some he found (1960) only on sphagnum bog mosses, not on forest mosses, e.g., *Nebela collaris, Centropyxis aculeata, Hyalosphenia papilio* (this again agrees with findings in my study). Others he found only on forest mosses, not on sphagnum bog mosses, e.g., *Corythion pulchellum, Trinema complanatum* (again in agreement with my present study).

He (1965) classifies the testacid amebas under five ecological categories: moss-dwelling, sphagnicolous, aquatic, terricolous or marine. He lists (1960, 1965) most *Arcella* spp. as aquatic (those I found in the bog must be so considered). Most *Difflugia* spp. and *Centropyxis* spp. he calls aquatic, but some are sphagnicolous, e.g., *D. pyriformis, D. globularis,* other species having aquatic, sphagnicolous and moss-dwelling varieties, e.g., *D. oblonga, D. aerophila,* and some being moss-dwelling, e.g., *D. rubescens, C. sylvatica.* Most *Nebela* spp. and *Hyalosphenia* spp. he calls sphagnicolous (I also found them so). Some *Euglypha* spp. he terms aquatic, e.g., *E. tuberculata,* some sphagnicolous, e.g., *E. cristata,* others moss-dwelling, e.g., *E. bryophila,* others ubiquitous, e.g., *E. laevis* (again my findings agree).

His study (1970, with Krizelj) indicates that certain species are likely to be found on a particular species of moss, e.g., *Difflugia lucida* only on *Eurhynchium striatum,* or *Centropyxis aerophila* only on *Ctenidium molluscum,* but other species on several mosses, e.g., *Difflugia oviformis* on 4 species of mosses (but *not* on another four species), most often on *Rhitidiadelphus triqueterus.* Still other species of testacid amebas were to be found on all eight species of mosses studied, e.g., *Nebela collaris.*

Clearly, the communities of Protozoa associated with various communities and species of mosses merit further study.

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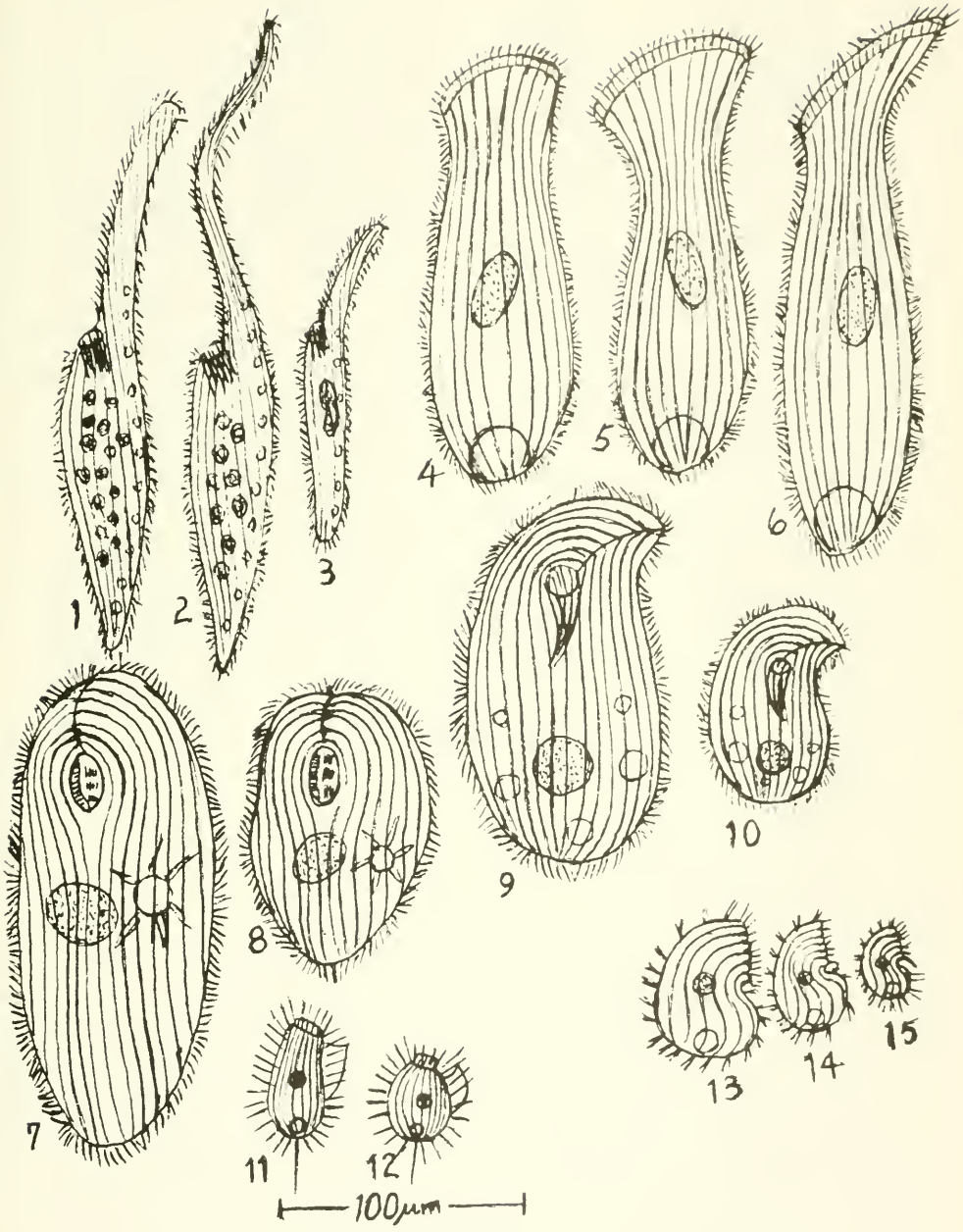

PLATE I. CILIOPHORA ASSOCIATED WITH MOSSES.

Figs. 1-3. *Dileptus* spp.; Fig. 1. *Dileptus anser*, cosmopolitan, found in sphagnum bogs; Fig. 2. *D. cygnus*, found in sphagnum bog, Fig. 3. *D. gracilis*, characteristic of wet forest moss. Figs. 4-6. *Spathidium* spp., Fig. 4. *S. spatula*, cosmopolitan, found in forest moss; Fig. 5. *S. amphoriforme*, characteristic of bog and forest mosses; Fig. 6. *S. muscicola*, characteristic of mosses, found in forest moss. Figs. 7-8. *Frontonia* spp.; Fig. 7. *F. leucas*, cosmopolitan, not found in this study. *F. depressa*, characteristic of mosses, found in sphagnum bog. Figs. 9-10. *Chilodonella* spp.; Fig. 9. *Chilodonella cucullulus*, cosmopolitan, found in sphagnum bog; Fig. 10. *C. wisconsinensis*, moss-dwelling, found in forest moss. Figs. 11-12. *Cyclidium* spp.; Fig. 11. *C. elongatum*, found in sphagnum bog; Fig. 12. *C. muscicola*, found in sphagnum and forest mosses. *C. terricola* (not shown), like *C. muscicola*, found on forest moss. Figs. 13-15. *Colpoda* spp.; Fig. 13. *C. cucullus* cosmopolitan, found in forest moss; Fig. 14. *C. inflata*, characteristic of mosses, found on forest moss; Fig. 15. *C. steini* cosmopolitan, found in sphagnum bog; *C. irregularis* and *C. penardi* (not shown), similar to *C. steini*, found on forest moss.

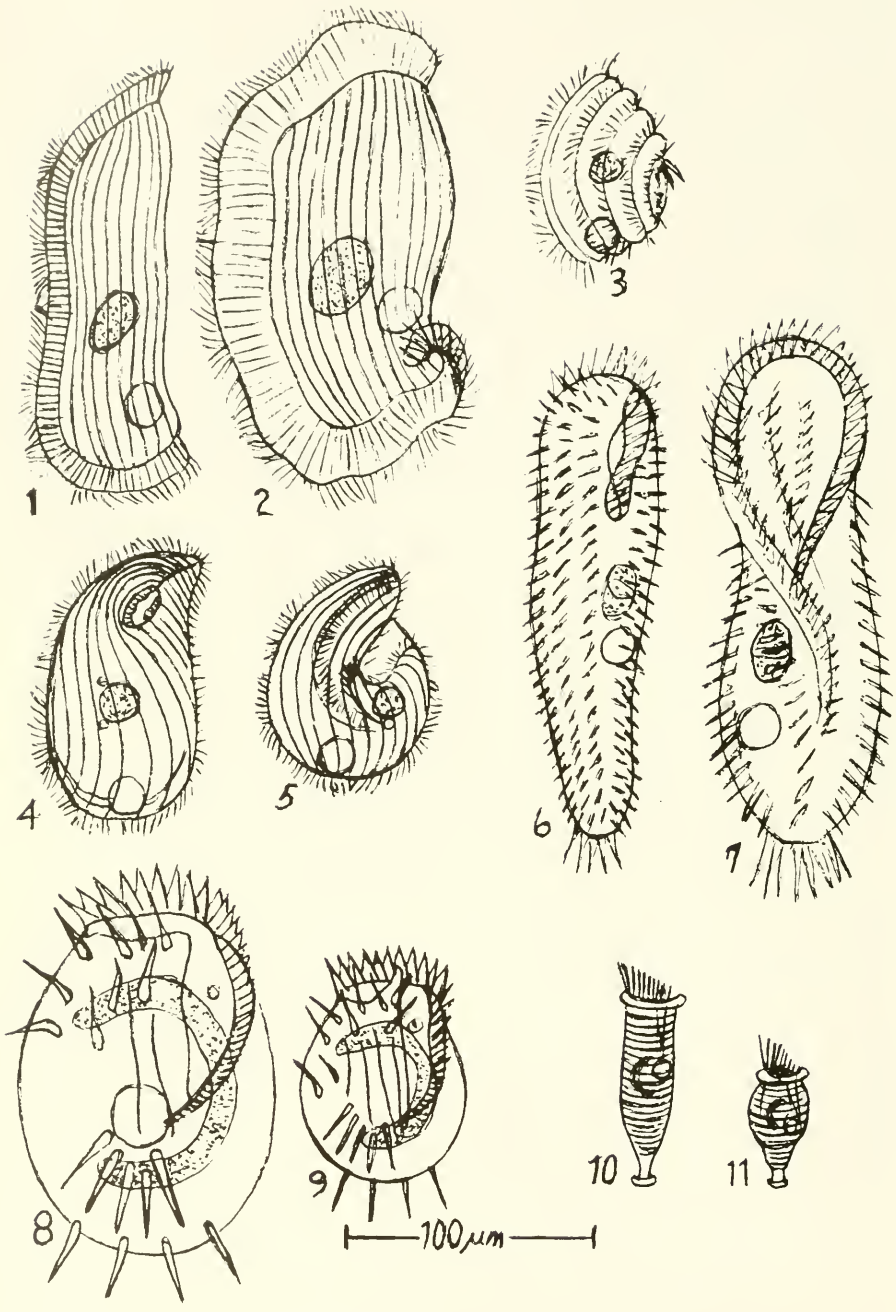

PLATE II. CILIOPHORA ASSOCIATED WITH MOSSES.

Fig. 1. *Loxophyllum* sp., from sphagnum bog. Fig. 2. *Bryophyllum sphagni*, characteristic of sphagnum bog. Fig. 3. *Leptopharynx sphagnetorum*, characteristic of sphagnum bog; another species (not shown, similar) on forest moss. Fig. 4. *Bryophrya* sp., characteristic of mosses, but not found in this study. Fig. 5. *Bresslaua baratiensis*, typical of forest moss, but not found here. Fig. 6. *Kerona rubra*, more or less cosmopolitan, found in sphagnum bog. Fig. 7. *Keronopsis helluo*, characteristic of mosses, found in sphagnum bog. Fig. 8. *Euplotes patella*, cosmopolitan, not found, shown here for comparison. Fig. 9. *Euplotes muscicola*, found in sphagnum bog. Fig. 10. *Rhabdostyla vernalis*, not found in this study, but shown for comparison. Fig. 11. *Rhabdostyla muscorum*, characteristic of mosses, found in forest moss.

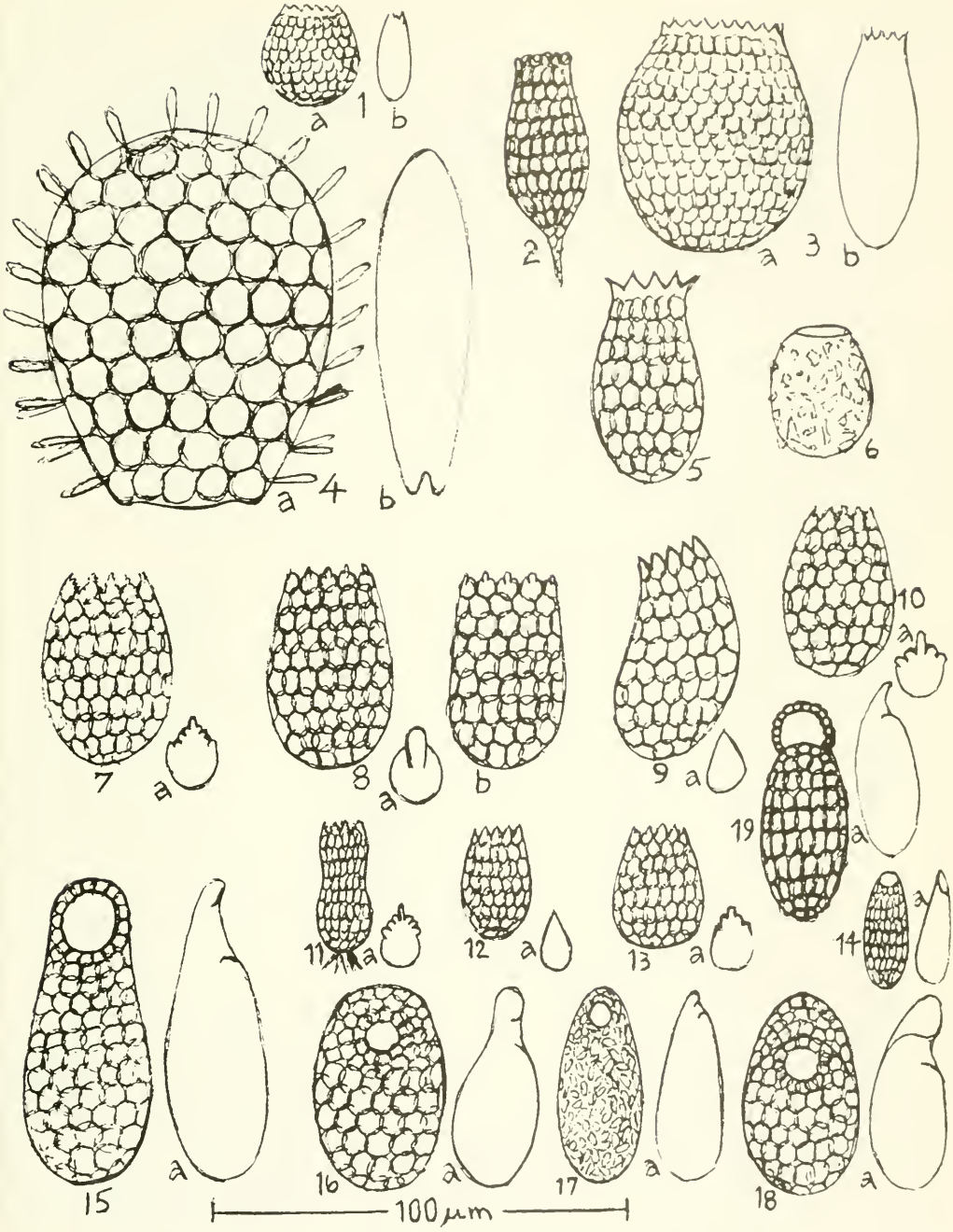

PLATE III. FILOSE TESTACID AMEBAS OF MOSSES (SHELLS ONLY).

Fig. 1. *Aussulina muscorum*, of forest mosses, *a*, broad view, *b*, edge view. Fig. 2. *Paraeuglypha* sp., from sphagnum bog. Fig. 3. *Assulina seminulum*, ubiquitous in mosses and forest soils, found in sphagnum bog, *a*, broad view, *b*, edge view. Fig. 4. *Placocista spinosa*, common in sphagnum bog; *a*, broad view, *b*, edge view. Fig. 5. *Tracheleuglypha dentata*, found in sphagnum bog. Fig. 6. *Pseudodifflugia compressa*, found in forest moss. Figs. 7-13. *Euglypha* spp.; Fig. 7. *E. strigosa*, *a*, detail of pseudostomal scale; on forest mosses; Fig. 8. *E. ciliata*, *a*, detail of pseudostomal scale; *b*, *E. ciliata* var. *glabra*, both of forest mosses; Fig. 9. *E. vanoyei*, *a*, detail of pseudostomal scale; Fig. 10. *E. umbilicata*, in sphagnum bog and on forest mosses, *a*, detail of pseudostomal scale; Fig. 11. *E. cristata*, on both sphagnum and forest mosses, *a*, detail of pseudostomal scale; Fig. 12. *E. laevis*, on both sphagnum and forest mosses, *a*, detail of pseudostomal scale; Fig. 13. *E. tuberculata*, on sphagnum, *a*, detail of pseudostomal scale. Fig. 14. *Corythion pulchellum*, on forest mosses, *a*, long section. Fig. 15. *Trinema lineare*, on sphagnum, *a*, long section. Fig. 16. *Trinema complanatum*, on sphagnum, *a*, long section. Fig. 17. *Corythion dubium*, on forest mosses, *a*, long section. Fig. 18. *Trinema penardi*, on sphagnum and forest mosses, *a*, long section. Fig. 19. *Trinema* sp. #4, in sphagnum mosses, *a*, long section.

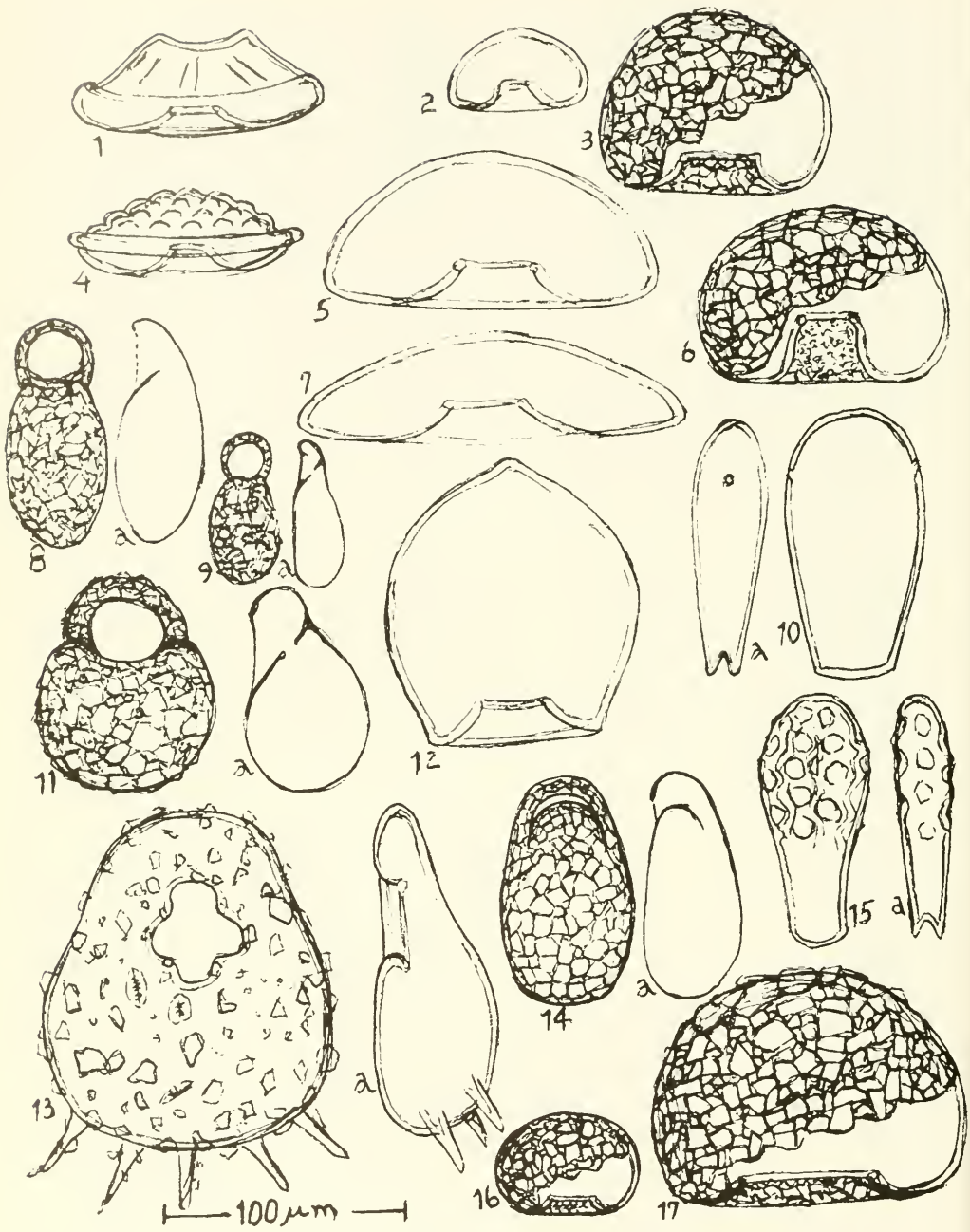

PLATE IV. LOBOSE TESTACID AMEBAS OF MOSSES (SHELLS ONLY).

Figs. 1,2,4,5,7,12. *Arcella* spp., side views; Fig. 1. *A. catinus*; Fig. 2. *A. hemisphaerica*; Fig. 4. *A. artocrea*; Fig. 5. *A. vulgaris*; Fig. 7. *A. discoides*; Fig. 12. *A. mitra*; *A. vulgaris*, cosmopolitan in fresh waters, others typical of sphagnum bog waters. Figs. 3,6,16,17. *Cyclopyxis* spp., side views; Fig. 3. *C. kahli*; Fig. 6. *C. puteus*; Fig. 16. *C. ambigua*, all on forest mosses; Fig. 17. *C. arcelloides*, cosmopolitan in forest situations, found in sphagnum bog. Figs. 8,9,11,13. *Centropyxis* spp. Fig. 8. *C. elongata*, *a*, long section; Fig. 9. *C. platystoma*, *a*, long section; Fig. 11. *C. sylvatica*, *a*, long section; all common on forest mosses, not on sphagnum; Fig. 13. *C. aculeata*, cosmopolitan in fresh waters, in sphagnum bog, but *not* in forest mosses. Figs. 10,15. *Hyalosphenia* spp., typical of sphagnum bog, not of forest mosses; Fig. 10. *H. papilio*, *a*, edge view; Fig. 15. *H. elegans*, *a*, edge view. Fig. 14. *Plagiopyxis callida*, *a*, long section, typical of forest situations, found in sphagnum bog.

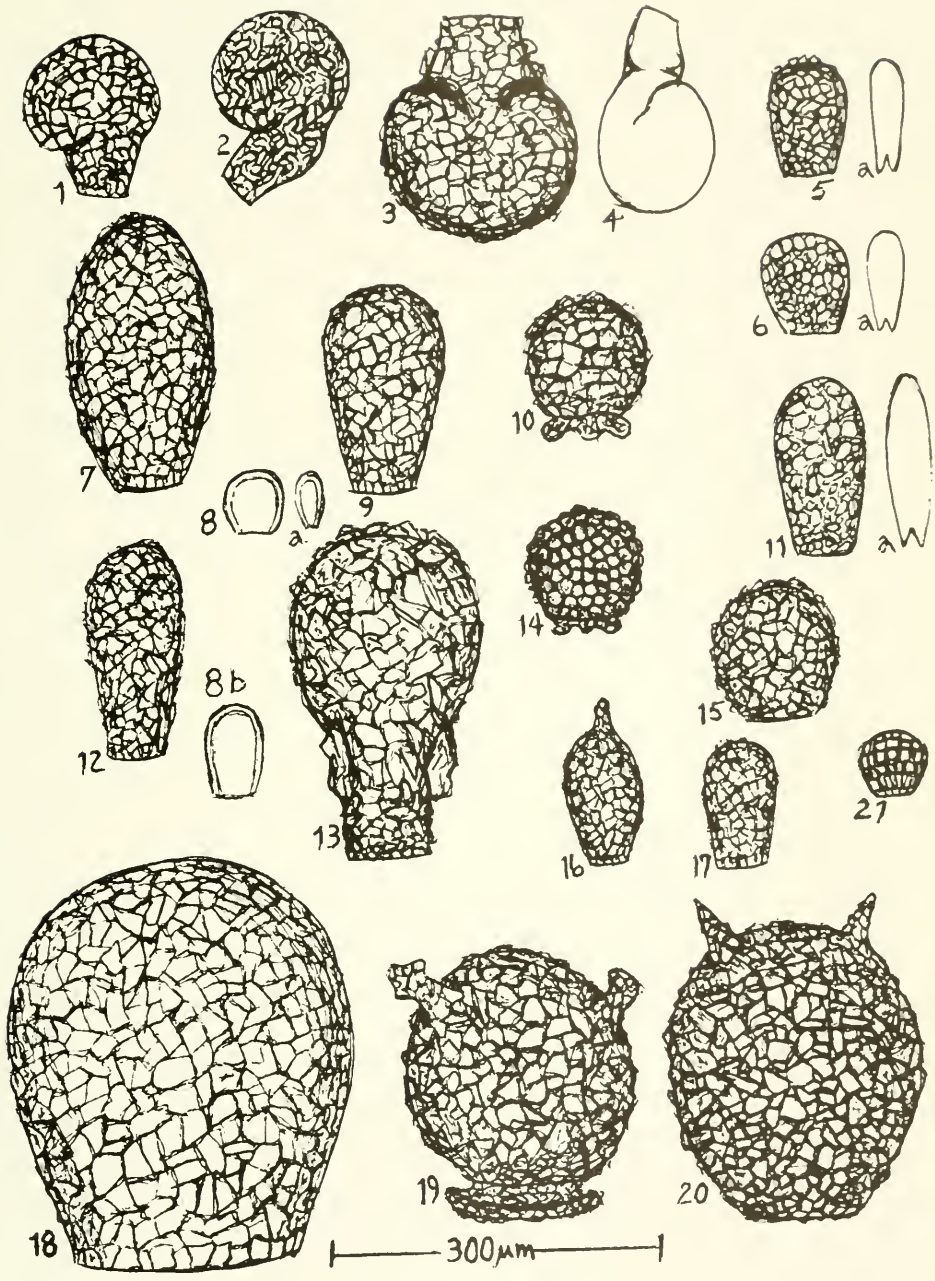

PLATE V. LOBOSE TESTACID AMEBAS OF MOSSES (SHELLS ONLY).

Figs. 1,2. *Lesquereusia* spp.; Fig. 1. *L. modesta,* found in forest mosses; Fig. 2. *L. spiralis,* found in sphagnum bog. Fig. 3. *Pontigulasia bigibbosa,* found in forest mosses. Fig. 4. Same, side view. Fig. 5. *Heleopora picta, a,* edge view, on sphagnum. Figs. 6,14,11. *Nebela* spp., typically moss-dwelling, found in sphagnum bog; Fig. 6. *N. bursaria, a,* edge view; Fig. 14. *N. tuberculata*; Fig. 11. *N. collaris, a,* edge view. Figs. 7,9,12,13,15-20. *Difflugia* spp.; Fig. 7. *D. tuscidula*; Fig. 9. *D. avellana*; Fig. 12. *D. oblonga*; Fig. 13. *D. pyriformis*; Fig. 15. *D. globulosa*; Fig. 16. *D. elegans*; Fig. 17. *D. fallax*; Fig. 18. *D. lebes*; Fig. 19. *D. olla*; Fig. 20. *D. bidens*; all found in sphagnum bog. Fig. 8. *Difflugiella minuta, a,* edge view; *b, D. oviformis*; both filose testacids from forest mosses. Fig. 14. *Cucurbitella* sp., from forest mosses. Fig. 21. *Paraquadrula discoides,* from forest mosses.

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SCIENCE BULLETIN

The Proboscis of the Long-Tongued Bees: A Comparative Study

By
MARK L. WINSTON

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The Proboscis of the Long-Tongued Bees: A Comparative Study[1]

Mark L. Winston

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ABSTRACT

The morphology and variation of the labiomaxillary complex in the long-tongued bees (families Apidae, Anthophoridae, Fideliidae, and Megachilidae) is described, including new characters, and the results applied to apoid taxonomy. Genera have been grouped by cladistic analysis into mouthpart groups, largely according to unique, shared, derived characters. This study supports a monophyletic origin for the long-tongued bees, with the Melittidae, or at least the genus *Ctenoplectra,* as a sister group. The Megachilidae are distinct from the other families. Among the Megachilidae, the Lithurginae diverge from the Megachilinae in labiomaxillary characteristics, and the Megachilini and Anthidiini are closely related, with the exception of *Dioxys,* which diverges from all other Megachilinae. Fideliids are grouped with the Anthophoridae and Apidae according to this analysis. Among the apids and anthophorids, close relationship between the Apidae and Xylocopinae is indicated, particularly between the Meliponinae and the Xylocopini. The allodapines form a distinctive group within the Xylocopinae, and elevation of these bees to tribal status may be justified. *Triepeolus* and *Thalestria* are distinct from the other Nomadinae, and reclassification of these may also be warranted. The position of *Canephorula* as a sister-group to the Eucerini is confirmed by mouthpart characteristics.

INTRODUCTION

Long-tongued bees (families Apidae, Anthophoridae, Fideliidae, and Megachilidae) have the glossa, labial palpi, and galeae as long as or longer than the stipites, and the first two segments of the labial palpi elongate, flattened, and sheathlike. Despite the functional significance and the many taxonomically useful characters of the labiomaxillary complex of bees, the morphology of and relationships indicated by bee mouthparts have been neglected in recent literature. The mouthparts of sphecoid wasps were described by Ulrich (1924), and various authors have described mouthparts of species of long-tongued bees (Michener, 1944, *Anthophora edwardsii;* Snodgrass, 1956, *Apis mellifera;* Camargo, 1967, *Melipona*

[1] Contribution number 1686 from the Department of Entomology, University of Kansas, Lawrence, Kansas 66045, U.S.A.

marginata; Iuga, 1968, *Bombus terrestris, lapidarius, agrorum*). Saunders (1890), Demoll (1908), and Correia (1973) compared mouthpart morphologies for certain genera of bees, and many authors have used some characteristics of bee mouthparts for taxonomic purposes.

The purposes of the present study are: 1) to describe the morphology and variation in the labiomaxillary complex of long-tongued bees, 2) to compare characteristic features of the mouthparts of representative genera, and 3) to use characters of the mouthparts for taxonomic purposes.

MATERIALS AND METHODS

The terms labiomaxillary complex, proboscis, and mouthparts are used interchangeably in this paper to refer to the combined labium and maxillae. The mouthparts of representative genera (Table 1) were removed from specimens, cleared in 10% KOH, washed in acetic acid, and preserved for study in glycerol. Unless otherwise noted, specimens were females. Examination was with a dissecting microscope, drawings were made of distinctive structures. Other species were examined in groups whose diversity justified such work.

For comparative purposes, the classification of Michener (1944, 1974a, Table 1) is used. Since the branching sequences suggested by mouthparts are often similar to those indicated by Michener, taxonomic names are used to identify mouthpart groups. When used in the context of mouthpart group rather than a taxon, the name is followed by the word "group." All members of a taxon are not necessarily members of the same mouthpart group; such cases are discussed in the text. A similar study being conducted by L. Greenberg is the source of most of the information concerning short-tongued bees discussed here.

Genera are placed in mouthpart groups largely according to the principles of cladistic analysis, as modified by Ashlock (1974), Michener (1974b), and Mayr (1976). The mouthpart groups should not be used alone to make the classification of long-tongued bees; they are meant to show only relationships as shown by mouthparts and may or may not be identical to groupings based upon other characters. Dendrograms (Figs. 18-22) are based on mouthparts of the forms examined by me; no doubt other characters would improve them, e.g., by reducing the number of multifurcations. Synapomorphous characters (Table 2) are indicated by numbers on the stems and parenthetically in the text.

Groups lacking synapomorphous characters in the mouthparts are indicated by dotted lines in the cladograms, following the classification of Michener (1944). In the text, the terms similarity, relationship, and affinity are used interchangeably in discussing phenetic closeness. Groups not characterized by synapomorphic characters may be monophyletic, but whether they are holophyletic or paraphyletic (sense of Ashlock, 1971) cannot be determined without consideration of other characters.

Table 3 shows the morphological terms used, sources for the terms (major works on apoid structure, not relating to priority), and other terms previously used. The terminology of Michener (1944) and Snodgrass (1956) is used when it agrees with current interpretations. Terms listed without sources but with previous terminology relate to structures previously described, but renamed here. Terms with neither sources nor previous nomenclature refer to structures to the best of my knowledge not previously described or named. In the text, names of structures are italicized where they are most fully described.

The labiomaxillary complex consists of the maxillae (laterally) and labium (medially) (Fig. 1). For purposes of description, the proboscis is considered to be extended downward. Thus, "anterior" refers to the surface that is then directed forward, equivalent to "dorsal" in papers that consider the proboscis to be extended forward.

Four representative views of mouthparts (Figs. 23-45) which best reveal important structures are used: a) outer view of the maxilla, b) inner view of the maxilla, c) posterior view of the labium, and d) anterior view of the labium. Stippling indicates membranous areas; dashed lines, sclerotized regions passing behind (in the view presented) others; and dotted lines, weakly sclerotized areas. Below are listed conventions used either for clarity or because certain structures were not examined in detail for all groups.

a) Outer view of the maxilla
   1) The basistipital process is not generally shown in this view, since it is usually obscured by the cardo. It is shown in the inner view.
   2) Only the basal end of the galea is usually shown, and no galeal hairs or ribbing are included.
   3) The basal end of the suspensory thickening is not shown.
   4) Only the apical ends of basally broken cardines are shown.
   5) Only basal segments of long maxillary palpi are shown.

b) Inner view of the maxilla
   1) The galea has been unfolded to reveal the midrib and basigaleal area.

c) Posterior view of the labium
   1) Only one half of the lorum, and parts of the associated cardo and basistipital process, are shown.
   2) The glossa is represented in repose, so that the paraglossae are retracted and are not shown. The glossal rod is drawn only when visible from a posterior view; annulations and hairiness of the glossa are only sche-

TABLE 1.

List of Specimens Examined, Classified According to Michener (1944, 1974) and Winston and Michener (1977).

- Megachilidae
  - Lithurginae
    - *Lithurge gibbosus*
    - *Lithurgommia wagenknechti*
    - *Trichothurgus dubius*
  - Megachilinae
    - Anthidiini
      - *Anthidiellum notatum robertsoni*
      - *Anthidium manicatum*
      - *Aztecanthidium xochipillium*
      - *Callanthidium illustre*
      - *Dianthidium ulkei*
      - *Dioxys productus subruber*
      - *Euaspis abdominalis*
      - *Heteranthidium bequaerti*
      - *Immanthidium repetitum*
      - *Hypanthidium taboganum*
      - *Nananthidium tamaulipanum*
      - *Odontostelis bivittata*
      - *Pachyanthidium bouyssoni*
      - *Paranthidium jugatorium perpictum*
      - *Parevaspis carbonaria*
      - *Spinanthidium wolkmanni*
      - *Stelis aterrima*
    - Megachilini
      - *Anthocopa copelandica*
      - *Ashmeadiella bucconis*
      - *Chalicodoma (Chelostomoides) angelarum*
      - *Chalicodoma (Chelostomoides) exilis*
      - *Chalicodoma cincta combusta*
      - *Chalicodoma rufipes*
      - *Chalicodoma torrida*
      - *Chelostoma fuliginosum*
      - *Chelostomopsis rubifloris*
      - *Coelioxys edita*
      - *Creightonella frontalis*
      - *Heriades carinata*
      - *Hoplitis albifrons argentifrons*
      - *Megachile albitarsis*
      - *Megachile frugalis pseudofrugalis*
      - *Noteriades* sp.
      - *Osmia lignaria*
      - *Osmia subaustralis*
      - *Proteriades deserticola*
- Fideliidae
  - *Fidelia* sp.
  - *Neofidelia profuga* (male)
- Anthophoridae
  - Nomadinae
    - *Biastes brevicornis*
    - *Caenoprosopis crabronina*
    - *Holcopasites heliopsis*
    - *Leiopodus lacertinus*
    - *Nomada annulata*
    - *Thalestria* sp.
    - *Triepeolus verbesinae*
  - Anthophorinae
    - Eucerini
      - *Eucera chrysopyga*
      - *Melissodes agilis*
      - *Peponapis crassidentata*
      - *Svastra atripes*
      - *Thygater amaryllis*
      - *Xenoglossa fulva*
    - Canephorulini
      - *Canephorula apiformis*
    - Melectini
      - *Melecta californica*
      - *Thyreus ramosa*
    - Centridini
      - *Centris poecila*
      - *Epicharis elegans*
    - Anthophorini
      - *Amegilla comberi*
      - *Anthophora cockerelli*
      - *Anthophora occidentalis*
    - Tetrapediini
      - *Tetrapedia* sp. (male)
    - Exomalopsini
      - *Ancyloscelis panamensis*
      - *Caenonomada bruneri*
      - *Exomalopsis zexmeniae*
      - *Tapinotapis caerula*
    - Ctenioschelini
      - *Ericrocis lata*
      - *Mesocheira bicolor*
    - Melitomini
      - *Diadasia afflicta*
      - *Melitoma segmentaria*
  - Xylocopinae
    - Xylocopini
      - *Lestis aeratus*
      - *Xylocopa brasilianorum varipuncta*
      - *Xylocopa fimbriata*
      - *Xylocopa v. virginica*
    - Ceratinini
      - *Allodape stellarum*
      - *Braunsapis facialis*
      - *Ceratina (Ceratinidia)* sp.
      - *Ceratina (Pithitis)* sp.
      - *Ceratina calcarata*
      - *Macrogalea candida*
      - *Manuelia gayi*
- Apidae
  - Apinae
    - Apini
      - *Apis dorsata*
      - *Apis mellifera*
  - Bombinae
    - Bombini
      - *Bombus pennsylvanicus*
      - *Psithyrus variabilis*
    - Euglossini
      - *Euglossa cordata* (male)
      - *Eulaema cingulata*
      - *Eupsia* sp. (male)
      - *Euplusia violacea*
  - Meliponinae
    - *Melipona fasciata*
    - *Melipona marginata*
    - *Melipona rufiventris*
    - *Meliponula bocandei*
    - *Trigona (Hypotrigona)* sp.
    - *Trigona capitata zexmeniae*
    - *Trigona chanchamayoensis*

TABLE 2.

SYNAPOMORPHOUS CHARACTERS OF THE MOUTHPARTS OF LONG-TONGUED BEES. See Figures 18-22 for dendrograms using these characters; the structures themselves are more fully described in the text.

1) mentum elongated and flared distally, articulating distally with the basal process of the prementum and basally with a v-shaped lorum (Figs. 1; 2c, d)
2) ligular arm distinct from prementum, with no region of continuous sclerotization between them (Fig. 14a, b)
3) basistipital process elongated
4) subligular process curved anteriorly (Fig. 13)
5) stipital comb present (Fig. 2a)
6) flabellum present at apex of glossa (Fig. 2c)
7) glossa with sclerotized rod extending its entire length
8) glossa, galea, and labial palpus as long or longer than stipes (Fig. 2)
9) galea with midrib (Fig. 2a)
10) ends of stipital sclerite not expanded (Fig. 6a)
11) stipital comb lost
12) dististipital process present (Fig. 7)
13) labial palpus with brush on cancavity of first segment (Fig. 11)
14) ligular arms ½ length of prementum or less (Fig. 14a)
15) lacinia with comb (Fig. 8c)
16) ligular arms secondarily fused with prementum (Fig. 14c)
17) inner cardinal process elongated (Fig. 3c)
18) basal process of prementum convexly curved (Fig. 10c)
19) inner and outer cardinal processes elongated (Fig. 3a)
20) subligular process separated from prementum by membranes (Fig. 12a)
21) brush on third segment of maxillary palpus (Fig. 6i)
22) expanded sclerotized region at junction of stipital and basistipital thickenings (Fig. 5e)
23) paraglossa at least ⅔ as long as glossa
24) subligular process expanded into U-shaped process (Fig. 12f)
25) paraglossa as long as glossa
26) striations in membrane underlying lacinia
27) area between subgalea and stipital sclerite partly sclerotized
28) prementum partly membranous and flattened (Fig. 12g)
29) brush on expanded lobe of the palpiger
30) bristles on membranous fold basad to the basigaleal area
31) subligular process as in Figure 12c
32) sclerotized ridge along outer margin of stipes (Fig. 4j)
33) stipital sclerite expanded apically into knob (Fig. 6d)
34) anterior longitudinal brace robust
35) both ends of stipital sclerite expanded to anterior edge of membrane lying between stipital sclerite and subgalea (Fig. 6i)
36) stipes with strong comb concavity, comb with robust, blunt teeth (Fig. 4h)
37) bipartite stipital thickening fused with stipital sclerite, with sclerotized area at junction of two sections of bipartite thickening (Fig. 5c)
38) basistipital process largely formed by expanded basistipital thickening (Fig. 5b)
39) stipital comb reduced, weak
40) bulla on inner cardinal process
41) lacinia hairless, membranous
42) transverse sclerotized ridge basal to cardinal process (Fig. 3e)
43) glossa, labial palpus, and galea much longer than stipes

matic. The apical portion of the glossa is not represented.

3) Only the basal segment (or a part thereof) of the labial palpus is represented.

d) Anterior view of the labium

1) Only one suspensory thickening is shown, and only its distal part.
2) The mentum and lorum are not represented.
3) Only one paraglossal suspensorium, paraglossa, and basal segment of the labial palpus are drawn, and one half of the basiglossal sclerite. These structures, as well as the glossa and ligular arms, are drawn in the extended position, contrary to that in the posterior view of the labium.

MORPHOLOGY OF THE LABIOMAXILLARY COMPLEX

Maxillae

The maxilla of the long-tongued bees retains the major structures of an insect maxilla (cardo, stipes, galea, lacinia, and maxillary palpus) but in modified form (Fig. 1). The cardo, stipes, and galea are elongated, and the stipes and galea are curved to sheath the labium when extended, features presumably important for nectar uptake. The

TABLE 3.

Nomenclature.

Structure	Source	Previous Terminology
Cardo	Michener (1944)	hémisternal (Iuga, 1968)
cardinal condyle	Snodgrass (1956)	.....
cardinal macula	.....	.....
inner and outer cardinal processes	.....	.....
Stipes	Michener (1944)	.....
stipital comb	Michener (1944)	.....
comb concavity	.....	.....
basistipital process	.....	apophyse cardinale (Iuga, 1968)
basistipital and stipital thickenings	.....	.....
dististipital process	.....	.....
stipital sclerite	.....	extensory rod (Snodgrass, 1956) subgaleal sclerite (Winston and Michener, 1977)
Lacinia	Michener (1944)	.....
Maxillary Palpus	Michener (1944)	.....
Galea	Michener (1944)	.....
blade	.....	postpalpal segment of galea (Michener, 1944)
subgalea	Snodgrass (1956)	prepalpal segment of galea (Michener, 1944)
basigaleal area	.....	.....
lorum	Snodgrass (1956)	submentum (Michener, 1944)
Mentum	Michener (1944)	.....
Prementum	Michener (1944)	sternum (Iuga, 1968)
basal process	.....	.....
subligular process	.....	distal plate (Snodgrass, 1956) subligular plate (Michener, 1944) sternal sclerite (Iuga, 1968)
Suspensory Thickening	.....	suspensory rod (Snodgrass, 1956) anterior conjunctival thickening (Michener, 1944)
Labial Palpus	Michener (1944)	.....
palpiger	Michener (1944)	.....
Ligular Arm	Snodgrass (1956)	héminotalia (Iuga, 1968)
Glossa	Michener (1944)	.....
flabellum	Michener (1944)	.....
salivary channel	Snodgrass (1956)	.....
Basiglossal Sclerite	.....	bonnet-shaped sclerite (Snodgrass, 1956) notal and basiglossal sclerites (Iuga, 1968)
Anterior Longitudinal Brace	Eickwort (1969)	.....
Paraglossa	Michener (1944)	.....
paraglossal suspensorium	.....	basiparaglossa (Iuga, 1968) ligular arm (Snodgrass, 1956)

lacinia is anterior to the stipes, near the food canal, and seems to function in closing that opening when the mouthparts are retracted.

The *cardo* (Figs. 2a, d; 3) is the slender, cylindrical suspensory sclerite in the lateral wall of the otherwise membranous basal part of the proboscis; it connects the maxillae and labium to the cranium. The cardo is usually slightly curved, commonly about two thirds as long as the stipes, but as short as half the stipital length in *Xylocopa*, or as long as the stipes in many genera. The

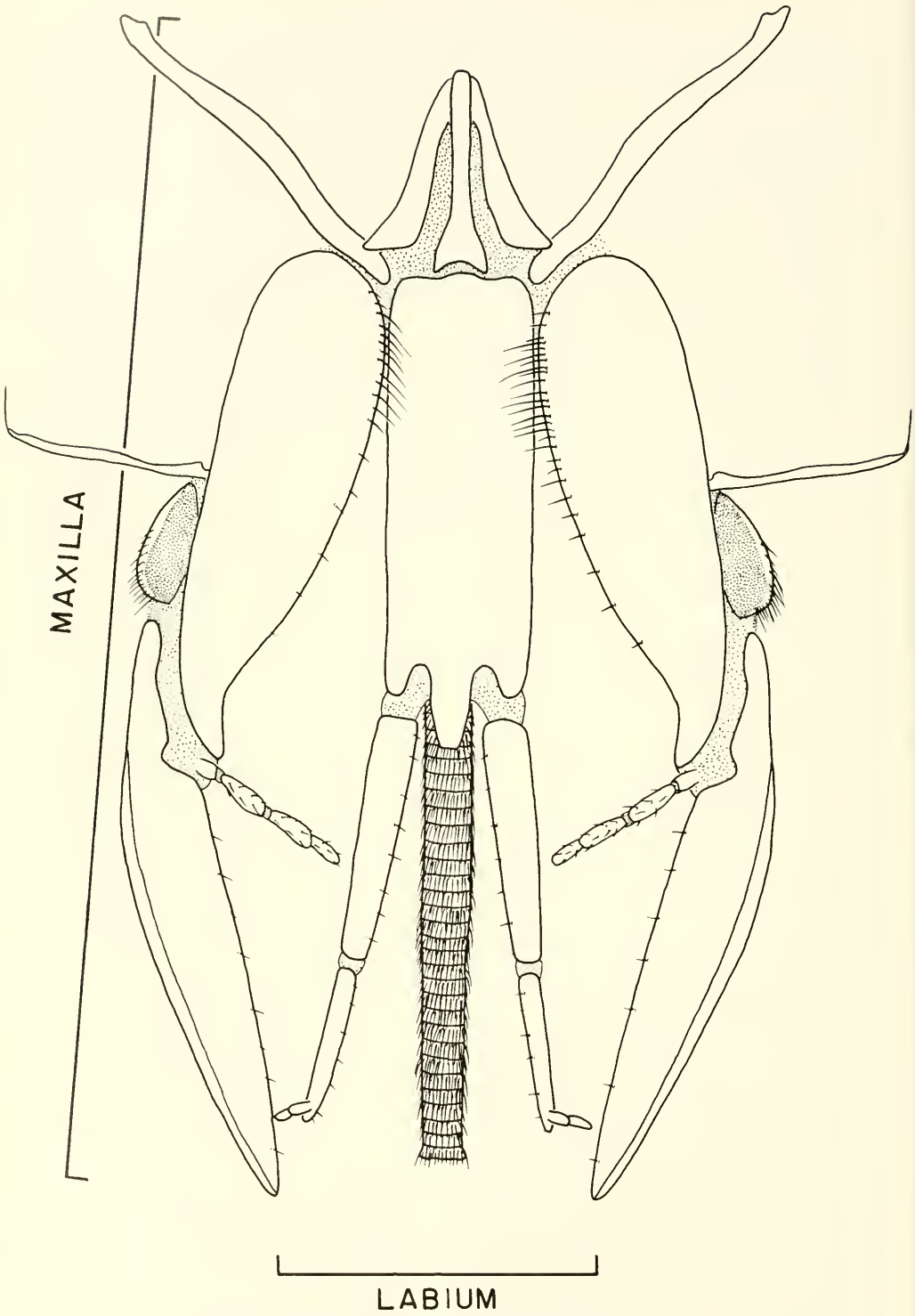


FIG. 1: Posterior view of generalized labiomaxillary complex.

cardo articulates basally with the cranium by the *cardinal condyle* (Fig. 2a); the basal terminus of the cardo extends beyond this condyle, and on this terminus is inserted the cardinal muscle, reaching to the wall of the head (Snodgrass, 1956), and the elevator muscle of the stipes, extending to the mid-region of the stipes (Iuga, 1968). In many genera, there is a cardinal macula midway along the inner surface of the cardo (Fig. 3b).

The distal end of the cardo is expanded into 2 processes, the *inner cardinal process* and the *outer cardinal process* (Figs. 2c, d; 3). The inner process curves mesad toward the mentum, perpendicular to it; the outer process curves outward toward the outer margin of the stipes. Generally one eighth to one half as long as the inner process, the outer one occasionally extends beyond the base of the stipes, forming, with the inner process, a bifurcate structure which rests upon the basistipital process (Fig. 3a) (19). The two cardinal processes connect the labium and the maxilla (Figs. 2c, d). The inner cardinal process articulates with the lorum, which is contiguous with the posterior edge of the inner process, and with the basistipital process which it overlaps. The outer cardinal process provides additional support for the cardinal-stipital articulation. In the Bombini, there is a heavily sclerotized tranverse ridge where the cardo divides into the two processes; this ridge may strengthen this area (Fig. 3e) (42). In *Apis,* there is a bulla on the inner cardinal process (Fig. 3f) (40).

The *stipes* (Figs. 2a, b; 4), a boat-shaped sclerite, extends distally along the sides of the prementum, articulating with the labium only through the cardo to the lorum, but connecting to the prementum by membrane basally. It is sclerotized on all but the inner anterior surface, forming a cavity which is closed by membranes and forms the channel in which blood and soft tissues reach the apical part of the maxilla. The stipes is two to five times as long as wide, often with a comb along the distal part of the posterior margin. The shape of the outer surface of the stipes varies considerably; some representative outer views are shown in Figure 4. The base is usually narrowed from both the anterior and posterior margins, although some genera have an expanded, antero-proximal, sclerotized flap (Fig. 4a). The apical end may be blunt (Fig. 4a), narrowed (Figs. 4c, e, f), or notched (Fig. 4g). Many genera have a sclerotized ridge medially along the outer surface of the apical third (Fig. 4j) (32).

The posterior margin of the stipes is often hairy, particularly proximally. The hairs vary in length (short, medium, long), abundance (absent, scarce, abundant, dense), and type (plumose, non-plumose, bristles) (Fig. 4). Occasionally, the anterior margin of the stipes may also be hairy, or even the entire outer stipital surface.

Most anthophorids and apids, and some megachilids (*Anthidium, Callanthidium,* and *Immanthidium*), have a *stipital comb* (Figs. 2a; 4) (5) along a well-sclerotized concave edge of the posterior distal margin of the stipes, the *comb concavity.* This concavity varies from weak (Fig. 4f) to strong (Fig. 4h), and in some species of meliponines is recessed behind the outer margin of the stipes (Fig. 4i). The bristles of the comb are generally robust, but some genera have weaker combs, with bristles attenuated distally and wide gaps between them. In *Xylocopa* and *Lestis* the bristles form extremely strong, blunt teeth (Fig. 4h) (36). Generally, stronger concavities contain stronger bristles. Some of the long-tongued bees without combs retain the comb concavity, occasionally with hairs in place of the comb. The stipital comb functions in cleaning and pollen manipulation (Schremmer, 1972; Jander, 1976).

The *basistipital process* (Figs. 2b, c, d; 5) is at the proximal end of the stipes. Despite its importance in the cardinal-stipital articulation, it has been neglected in the literature; only Iuga (1968) mentions it as the "apophyse cardinale." I have renamed it since it is an extension of the stipes. It is formed by merged proximal extensions of the base of the outer margin and the sclerotized inner anterior edge of the stipes, the basistipital thickening. The basistipital proc-

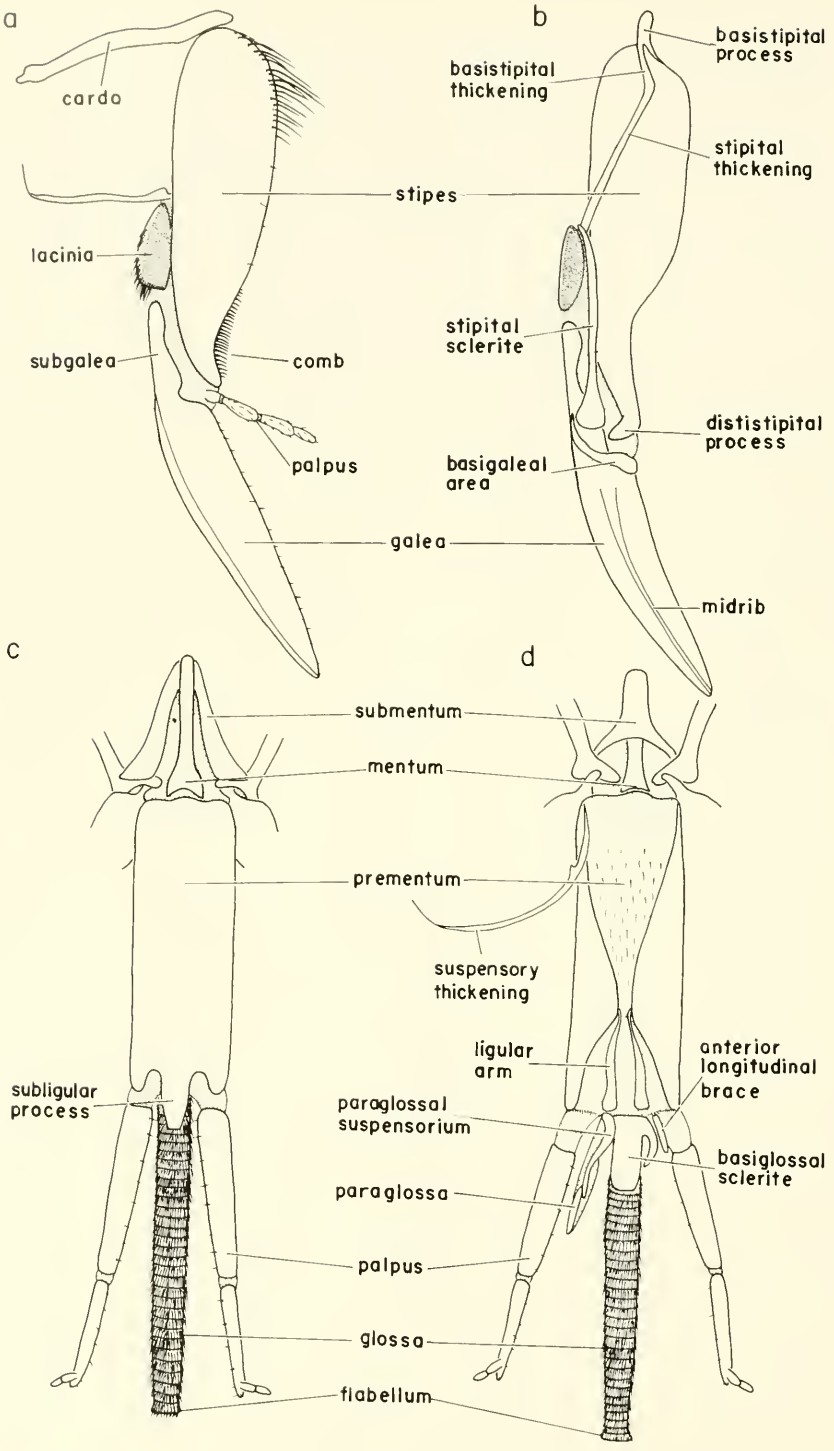


FIG. 2: Representative views of generalized labiomaxillary complex, showing nomenclature of structures. a) outer view of the maxilla, b) inner view of the maxilla, c) posterior view of the labium, d) anterior view of the labium.

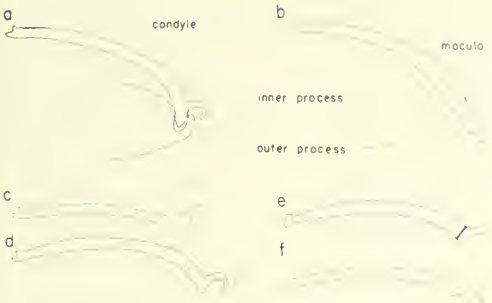


FIG. 3: Cardines of selected genera. a) *Neofidelia*, b) *Anthophora*, c) *Holcopasites*, d) *Caenonomada*, e) *Bombus*, f) *Apis*.

ess extends mesad and curves under the inner cardinal process, being mostly obscured in an outer view of the stipes. In some genera it extends beyond the inner cardinal process, and abuts against the inner edge of the lorum. In many meliponines, the basistipital process is separated from the outer margin of the stipes, and is formed largely by the extension of the basistipital thickening (38). It is also expanded apically as a distinct sclerotized pad which abuts against the lorum (Fig. 5b). It is similar to this in the Bombini, but partly formed by the outer margin of the stipes. Membranes loosely connect the basistipital process and the inner cardinal process, allowing free longitudinal movement of the maxilla and, through the articulation between the cardo and the lorum, of the labium as well.

Basally the inner surface of the stipes is narrower than the outer surface so that, in an inner view, the anterior part of the outer stipital wall can be seen (Fig. 2b). The anterior edge of the inner surface is thickened basally, forming the well sclerotized *basistipital* and *stipital thickenings* (Figs. 2b; 5). The basistipital thickening forms and reinforces the posterior edge of the basistipital process. The stipital thickening extends from the distal end of the basistipital thickening to a point midway along the stipes and is one to three times as long as the basistipital thickening. In *Thalestria* and *Triepeolus* the two thickenings meet at an expanded sclerotized area (Fig. 5e) (22). Apically, the stipital thickening extends beyond the edge of the body of the stipes (Fig. 2b), abutting against the proximal end of the stipital sclerite and fusing with it in many genera (Fig. 5c, d). While the stipital thickening is usually straight or smoothly curved (Fig. 2b), it sometimes has two sections (referred to here as bipartite), as in the Xylocopinae and some Apidae (Fig. 5c) (37). The sclerotization of the stipital thickening probably strengthens the connection between the stipes and the stipital sclerite.

The *stipital sclerite* (Figs. 2b; 6) is a slender sclerite on the inner side of the maxilla close to the inner edge of the stipes, extending from the basigaleal area to the distal end of the stipital thickening. Usually curved, it is separable from the stipes in all but *Xylocopa brasilianorum* and *X. fimbriata*, in which it is well-attached to the inner anterior edge of the stipes and overlapped by membranes (Fig. 38). The suspensory thickening is connected by membranes to the proximal end of the stipital sclerite and links the prementum and maxilla. In many genera, either the apical end or proximal end of the stipital sclerite, or both, are expanded as triangular or rounded

FIG. 4: Stipites of selected genera. a) *Eucera*, b) *Chalicodoma*, c) *Stelis*, d) *Anthophora*, e) *Mesocheira*, f) *Tetrapedia*, g) *Neofidelia*, h) *Xylocopa*, i) *Melipona*, j) *Evomalopsis*, k) *Anthidiellum*.

processes (Fig. 6) (33, 35). An oval membranous area connects the subgalea, stipital sclerite, and the lacinia; in some anthophorids, it is partly sclerotized (27). Snodgrass (1956) calls the stipital sclerite the extensory rod, and it presumably is involved in movements of the lacinia and the galea. It has also been called the subgaleal sclerite by Winston and Michener (1977), who thought it to be derived from the inner edge of the subgalea, but L. Greenberg (in prep.) shows it to be fused with the stipes in sphecoid wasps and many short-tongued bees, suggesting a derivation from the inner distal margin of the stipes.

All megachilids except *Dioxys* have a *dististipital process* (Figs. 2b; 7) (12) perpendicular to the distal end of the stipes, extending anteriorly. It is a short distal bulge in some genera (Fig. 7a); in others it extends across the galeal-subgaleal junction toward the anterior edge of the galea (Fig. 7b). Its function is not clear. Since the galeal-subgaleal junction rests upon it, it

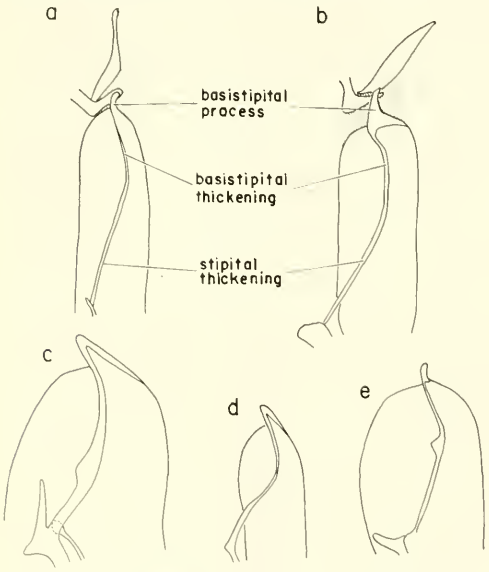


FIG. 5: The basistipital process and stipital and basistipital thickenings of selected genera. a) *Dioxys*, b) *Melipona*, c) *Xylocopa*, d) *Nomada*, e) *Triepeolus*.

may help to move the galea, perhaps as a rod against which the galea can be pulled into the folded resting position.

The *lacinia* (Figs. 2a, b; 8) is a partly sclerotized or sometimes membranous lobe

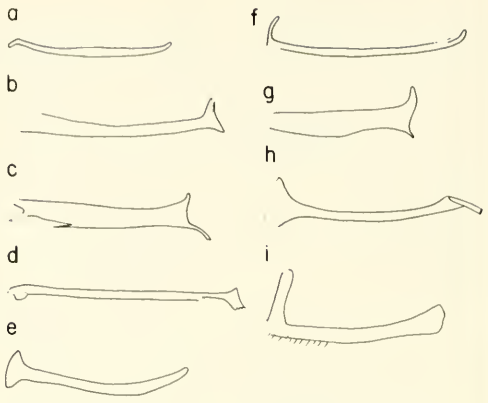
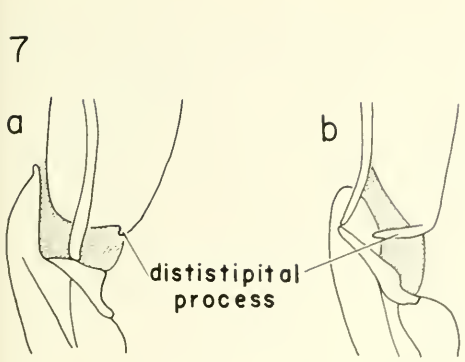


FIG. 6: Stipital sclerites of selected genera. a) *Megachile*, b) *Euplusia*, c) *Apis*, d) *Ceratina*, e) *Tetrapedia*, f) *Diadasia*, g) *Anthophora*, h) *Bombus*, i) *Melipona*.

midway along the anterior edge of the stipes, basal and mesal to the subgalea. Membranes connect its base to the base of the stipital sclerite and to the suspensory thickening, which passes immediately basal to the lacinia. Its anterior edge is usually well-sclerotized (Figs. 8a, b), with sclerotization sometimes extending posteriorly along the distal edge as well (Figs. 8c, d). The regions supporting the sclerotized edges of the lacinia are membranous; in *Apis*, the entire lacinia is membranous (Fig. 8e) (41). In most anthidiines and in *Coelioxys*, there is a lacinial comb along the distal (and sometimes anterior) edge, made up of straight, relatively robust bristles (Figs. 8c, d) (15). In other genera the anterior sclerotized areas of the laciniae are unusually hairy, the hairs ranging from sparse (Fig. 8f) to abundant (Fig. 8a). Some genera (such as *Apis*, Fig. 8e) lack all lacinial hairs (41).

The *maxillary palpus* (Figs. 2a, b) of 1-6 segments arises from a membranous area immediately distal to the apex of the stipes. The basal segment is generally broader than the distal ones. The palpus is often hairy, occasionally with bristles. There is a brush on the third segment in *Melitoma* and *Diadasia* (Figs. 11b; 43) (21).

The *galea* (Figs. 2a, b) is a long, thin, tapering blade, convex on the outer surface and concave on the inner, posterior surface. It arises from the distal end of the stipes,



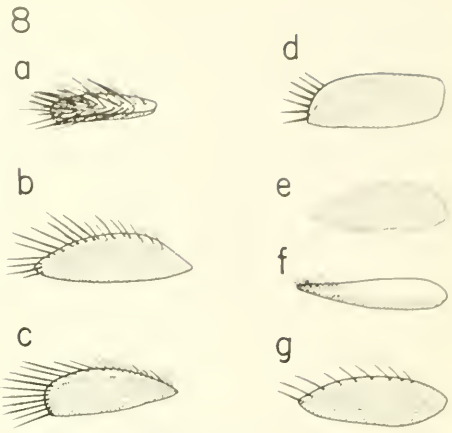


FIG. 7: *Dististipital process of selected* genera. a) *Lithurge*, b) *Hypanthidium*.

FIG. 8: Laciniae of selected genera. a) *Xylocopa*, b) *Stelis*, c) *Hypanthidium*, d) *Coelioxys*, e) *Apis*, f) *Osmia*, g) *Hoplitis*.

and is divided into two regions, the postpalpal *blade* and the much shorter, prepalpal, triangular *subgalea* (Fig. 2a). Between the galeal blade and the subgalea, where the galea bends backwards in repose, the galea is narrowed. This narrowed region is strengthened on the inner, concave surface by the *basigaleal area* (Figs. 2b; 9), a region of heavier sclerotization generally extending along the basal edge of the blade, more or less transverse to the main axis of the galea. A prominent *midrib* extends the length of the blade (9), as a fold in the inner galeal wall, often supported basally by the anterior edge of the basigaleal area. Hairs often arise from the midrib, sometimes extending to the edge of the galea. The blade is well-sclerotized basally, often less so distally. The distal area of lighter sclerotization often appears ribbed, probably due to channels through the sclerotic material that connect hairs on the edges of the galea to the region of the midrib.

Labium

The labium of long-tongued bees can be divided transversely into three regions, the postmentum, prementum, and ligula (glossa, paraglossa, and labial palpus) (Fig. 1). The prementum is between the stipites; the glossa, paraglossa, labial palpus, and associated sclerites are articulated at its apex. The sclerites of the postmentum (lorum and mentum) connect the base of the prementum to the maxillae. Michener (1944) noted misinterpretations which confused the mentum with the submentum, and the prementum with the mentum. As there is either one or no postmental plate in other Hymenoptera (Kirkmayer, 1909; Duncan, 1939), the lorum may be a secondarily derived structure not homologous with the primitive insect submentum. I use the term mentum to designate the distal sclerite of the postmentum.

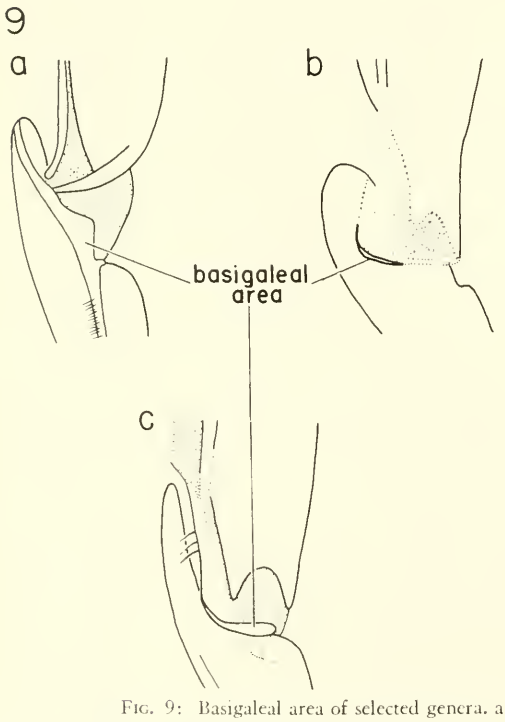
The proximal sclerite of the postmentum, the lorum (submentum of some authors) is v-shaped, with its divergent arms articulated to the distal ends of the maxillary cardines as previously described (Figs. 2c, d). Its medial region articulates with the distal sclerite of the postmentum, the *mentum*, the proximal end of which curves over the lorum (Figs. 2c, d). The mentum is elongate, thin, and flared distally where it connects with the prementum. The distal margin of the apical expansion of the mentum may be slightly concave (Fig. 10a), concave (Fig. 10b), bifurcated (Fig. 10c), notched (Fig. 10d), or reduced (Fig. 10e), and articulates with the base of the prementum (Figs. 2c; 10). The connections of the lorum to the maxillary cardines and the prementum through the mentum, allow the labiomaxillary complex to be protracted and retracted as a single unit. At least in *Apis*, the protractor muscles insert on the maxillae, the retractor muscles on the labium, so that movements of the maxillae and the labium

are completely interdependent (Snodgrass, 1956).

The labiomaxillary complex is strengthened basally by the *suspensory thickenings* (Figs. 2a, d), a pair of ribbon-like bands in the anterior conjunctiva of the proboscis (the anterior conjunctival thickenings of Michener, 1944). The distal end of each thickening connects to the anterior surface of the prementum near the base. From there it extends to the inner edge of the lacinia, then curves anteriorly, supporting the conjunctiva, passing lateral to the mouth before turning toward the paramandibular process of the hypostoma (Michener, 1944). The sclerotization of the suspensory thickening is often expanded where it curves anteriorly; this expanded area may represent the fusion of the two segments of the suspensory thickening present in short-tongued bees (except Melittidae, R. McGinley, pers. comm.). Membrane connects this area to the lacinial-stipital junction, further linking the labium with the maxillae.

The *prementum* (Figs. 2c, d) is an elongated sclerite, usually slightly wider distally than proximally, located between the two stipites. It is convex posteriorly and concave anteriorly, the concavity being closed by membrane, continuous with the labiomaxillary tube, and containing the muscles of the glossa and paraglossae (Michener, 1944). The articulation with the mentum is by means of the basal process of the prementum (Fig. 10), a usually concave expansion of the base of the prementum. In some genera the base is convex (Fig. 10c) (18) or reduced (Fig. 10e). Distally, the posterior premental surface is trilobed, the outer lobes contiguous with the labial palpi, the central lobe forming the subligular process. In *Canephorula,* the prementum is partly membranous (Fig. 12g) (28).

The *labial palpus* (Figs. 2c, d) articulates with the outer apical lobe of the prementum through the largely membranous *palpiger* (Fig. 2c), which sometimes is strengthened by a narrow longitudinal sclerotic slip. The



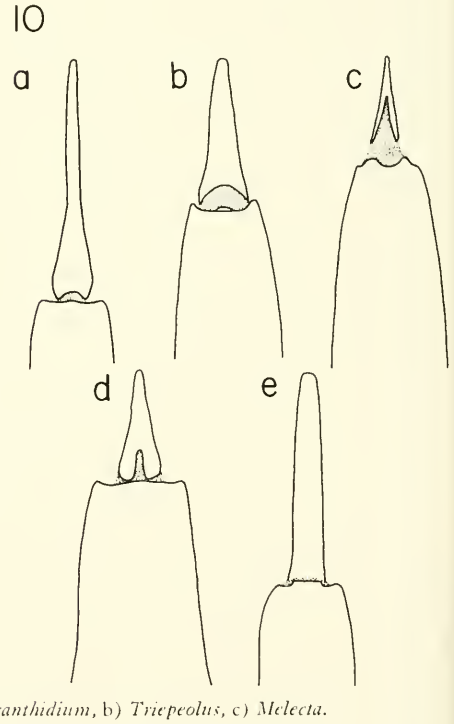


FIG. 9: Basigaleal area of selected genera. a) *Heteranthidium,* b) *Triepeolus,* c) *Melecta.*

FIG. 10: Menta of selected genera, showing variation in distal end. a) *Eucera,* slightly concave, b) *Dioxys,* concave, c) *Nomada,* bifurcate, d) *Lithurge,* notched, e) *Exomalopsis,* reduced.

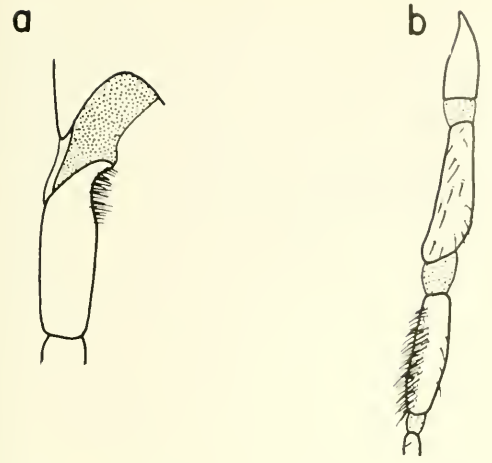


FIG. 11: a) Brush on first labial palpal segment of *Lithurge*, b) Brush on third maxillary palpal segment of *Diadasia*.

palpus consists of four segments separated by membranes. The two basal segments are elongate, flattened, and concave on the inner surfaces so as to sheath the glossa. These two segments are well sclerotized medially, with lighter sclerotization along the lateral margins. The relative lengths of the basal segments vary. The two distal subcylindrical segments arise subapically on the second segment, and project almost perpendicularly to it. The labial palpus is often hairy, sometimes bristly. The Lithurginae have a brush on a concavity of the proximal inner edge of the first segment (Fig. 11a) (13). There is a small brush on an expanded, sclerotized lobe of the palpiger in *Melecta* and *Thyreus* (Fig. 33) (29).

The base of the glossa is supported posteriorly by the *subligular process* (Figs. 2c; 12), which extends distally from the apex of the prementum, curving anteriorly at its apex, perpendicular to the glossa (Fig. 13) (4). In the *Anthophora* group, it extends to form a u-shaped process upon which the glossa rests (Fig. 12f) (24). In a few genera the subligular process is separated from the apex of the prementum by a narrow membranous area (Fig. 12a) (20). Fig. 12 shows representative configurations of the subligular process.

On the anterior surface of the prementum, the two *ligular arms* (Figs. 2d; 14) are located lateral to the base of the glossa. Each is a narrow sclerite, slightly expanded apically, extending from midway along the prementum almost to its apex, except in the Lithurginae, where the ligular arm extends nearly to the base of the prementum (Fig. 14b). Each incurved lateral margin of the prementum (or premental fold) has a region of expanded sclerotization at the base of the ligular arm; in the Apidae, Anthophoridae, and Fideliidae, the base of the ligular arm merges with this sclerotized area (Fig. 14c) (16). In the Megachilidae, the ligular thickening is not continuous basally with the sides of the prementum, but is the concave anterior surface of the prementum, connected to the sides of the prementum by membranes (Fig. 14a). When the glossa is retracted, its base rests between the ligular arms. When protracted, the base of the

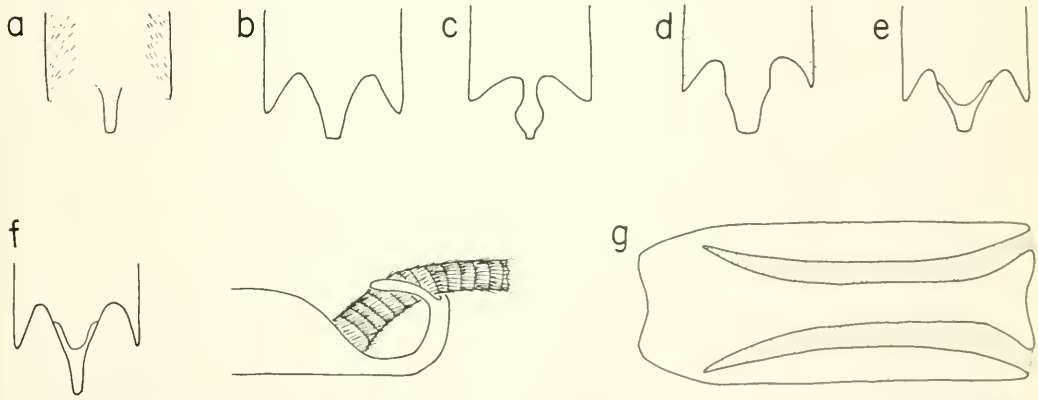


FIG. 12: Subligular processes of selected genera. a) *Neofidelia*, b) *Svastra*, c) *Tetrapedia*, d) *Holcopasites*, e) *Exomalopsis*, f) *Anthophora* (with lateral view), g) *Canephorula* (whole prementum).

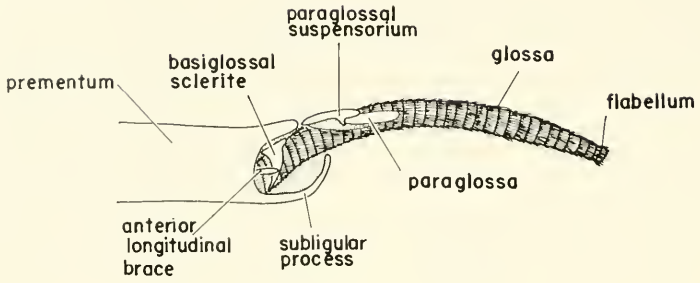


FIG. 13: Lateral view of generalized ligular region and glossa.

glossa extends beyond the apices of the ligular arms. In Megachilidae the ligular arms can move slightly in the same direction as the glossa; this mobility may increase the distance that the glossa can be protracted.

The *glossa* (Figs. 2c, d; 13), arises at the apex of the prementum, as a fusion product of the primitive, paired glossae (Snodgrass, 1956; Michener, 1944). It is usually slightly longer than the prementum, and densely hairy, split posteriorly by a longitudinal medial groove, the *salivary channel* (Snodgrass, 1956). A flexible rod extends the length of the inner wall of the salivary channel (7), although it is often only apparent in a cross-section. Transverse rows of setae alternate with bare areas, giving the glossa a ringed appearance. At its apex the glossa is expanded into the flabellum (Fig. 2c) (6). (Since a systematic study of glossal cross-sections was not done, variation in the salivary channel, rod, and flabellum is not a part of this study). In the euglossines, the glossa is greatly elongated (as are the labial palpi and the galea), sometimes extending well beyond the tip of the abdomen (43).

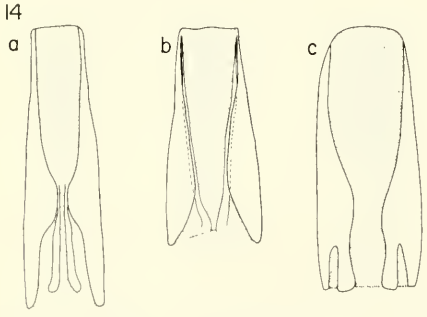


FIG. 14: Ligular arms of selected genera, showing three major types. a) *Stelis* (short, distinct from prementum), b) *Lithurge* (elongate, not fused with prementum), c) *Apis* (short, fused with prementum).

The *basiglossal sclerite* (bonnet-shaped sclerite, Snodgrass, 1956; notal and basiglossal sclerites, Iuga, 1968) (Figs. 2d; 15) partly encloses the base of the glossa antero-laterally. Laterally, it forms two thin processes extending posteriorly that appear like the tie strings of a bonnet. Lateral to the basiglossal sclerite, on the inner side of the paraglossal suspensorium, are two short sclerites, the *anterior longitudinal braces* (Fig. 13), present in many but not all genera.

Lateral to the glossa are the two *paraglossae,* elongate lobes each arising on a paraglossal suspensorium at the base of the glossa (Figs. 2c; 13; 16). The paraglossa varies from mostly sclerotized to mostly membranous, commonly largely membranous, often concave mesally and fitting snugly against the posterior glossal surface. Usually less than one quarter the length of the glossa, in some genera (Eucerini, Melectini, *Canephorula*) paraglossae extend the length of the glossa (23, 25). They are occasionally hairy.

The *paraglossal suspensorium* (basiparaglossa of Iuga, 1968), a sclerotized base for the paraglossa lateral to the base of the glossa, has a posteriorly directed arm upon which the paraglossa arises. In the Xylocopinae, Apidae, and some Exomalopsini,

the paraglossa is broadly attached to the paraglossal suspensorium (Fig. 16a), while in other genera the articulation is narrow (Fig. 16b). Snodgrass (1956) considered the paraglossa to arise from an apical extension of the ligular arm, thinking that the paraglossal suspensorium was part of the ligular arm. However, when the proboscis is protracted, the paraglossal suspensorium and the paraglossa move with the glossa, while the ligular arm remains stationary; thus the paraglossal suspensorium is clearly a separate sclerite. At rest, the base of the glossa, the paraglossae, and the paraglossal suspensoria lie between the ligular arms.

Movement of the Labiomaxillary Complex

The protraction and retraction of the labiomaxillary complex has been described for *Anthophora edwardsii* (Michener, 1944) and *Apis mellifera* (Snodgrass, 1956). When at rest, the proboscis is folded below the head, in three sections, in a z-shaped pattern. The basal section, containing cardines, lorum, and mentum, is directed posteriorly, and articulates with the head through the cardinal condyles. The midsection, made up of the stipites and prementum, folds anterior beneath the cardines. The third section (glossa, paraglossae, labial palpi, and galeae) rests beneath the stipites and prementum and folds posteriorly towards the neck.

As mentioned above, retraction and protraction in *Apis* depends on maxillary protractor muscles and labial retractor muscles, the proboscis rocking in and out on the articulations of the cardines with the head. When extended, the glossal section bends anteriorly until almost in line with the stipites and prementum, while the cardines, mentum, and lorum move forward until they are below the maxillary processes of the head. The galeae and labial palpi support the distal part of the glossa, while the basiglossal sclerite, ligular arms, subligular process, paraglossae, and paraglossal suspensoria support the base. Snodgrass (1956) describes the sucking action of the proboscis.

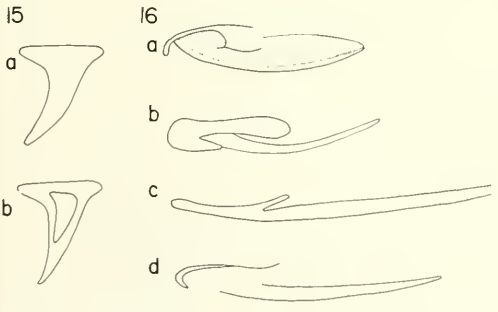


Fig. 15: Basiglossal sclerites of selected genera. a) *Melipona,* b) *Anthidium.*

Fig. 16: Lateral views of the paraglossa and paraglossal suspensorium of selected genera. a) *Exomalopsis* (broadly attached), b) *Centris* (not broadly attached), c) *Thygater,* d) *Thyreus.*

COMPARATIVE STUDY

Long-tongued bees are distinguished from short-tongued bees by many characters. (The following discussion excludes the short-tongued bee *Ctenoplectra;* see below.) The prementum, glossa, first two segments of the labial palpus, and galea of long-tongued bees are longer relative to other mouthpart structures than in short-tongued bees (8). Although some short-tongued bees have an elongated glossa (e.g., *Thrinchostoma*), or elongated prementum and stipites (e.g., many halictines), there are no species with the combination of elongated labiomaxillary structures listed above. In long-tongued bees, the lorum is V-shaped and the mentum is elongated and narrow, especially basally (1). In short-tongued bees, the lorum is not V-shaped, but is broad (except in the melittids, where lorum and mentum closely resemble those of the long-tongued bees), or reduced or absent in some halictids. The mentum (again with the exception of melittids) is relatively short, and generally broader than in long-tongued bees, or is sometimes more or less membranous or absent.

Other distinguishing structures of long-tongued bees are important in the support and function of the elongate proboscis. The glossa has a terminal flabellum (6) and an internal sclerotized rod (7), both absent in the short-tongued bees. Other characters not found in the short-tongued bees are the anterior curving of the subligular process (4), which could act to support the glossa, and the presence of the galeal midrib

(9), important in strengthening the galea which sheathes the extended glossa. The sclerotized ridge on the inner surface of the galea in some short-tongued bees may be homologous with the galeal midrib of the long-tongued bees.

The two groups of bees also differ in the location of maxillary combs. Short-tongued bees often have a comb on a sclerotized plate of the inner galeal wall (Fig. 17), perhaps corresponding to the galeal comb of sphecoid wasps. This plate is probably homologous with the basigaleal area of long-tongued bees (Figs. 2b; 9). However, long-tongued bees have no galeal comb, although Jander (1976) suggests that rudiments of a galeal comb may be present in *Ceratina* (none has been found in this study). Many genera of long-tongued bees do have a comb on the posterior edge of the distal part of the stipes (Fig. 2a) (5), absent in all short-tongued bees except *Ctenoplectra* (Melittidae). Jander (1976) suggests that the galeal and stipital combs are equifunctional, involved in cleaning movements of the foreleg, homologous to similar cleaning movements of most other Hymenoptera.

Many other characteristics of certain groups of long-tongued bees appear to be derived from more primitive, short-tongued ancestors. The inner and outer cardinal processes of short-tongued bees, as well as the basistipital process, are usually short; their elongation in some long-tongued genera is probably derived. The stipital sclerite of short-tongued bees is variable, but usually expanded basally, apically, or both; reduction of these expansions presumably also is a derived condition. Moreover, short-tongued bees have no dististipital process, lacinial

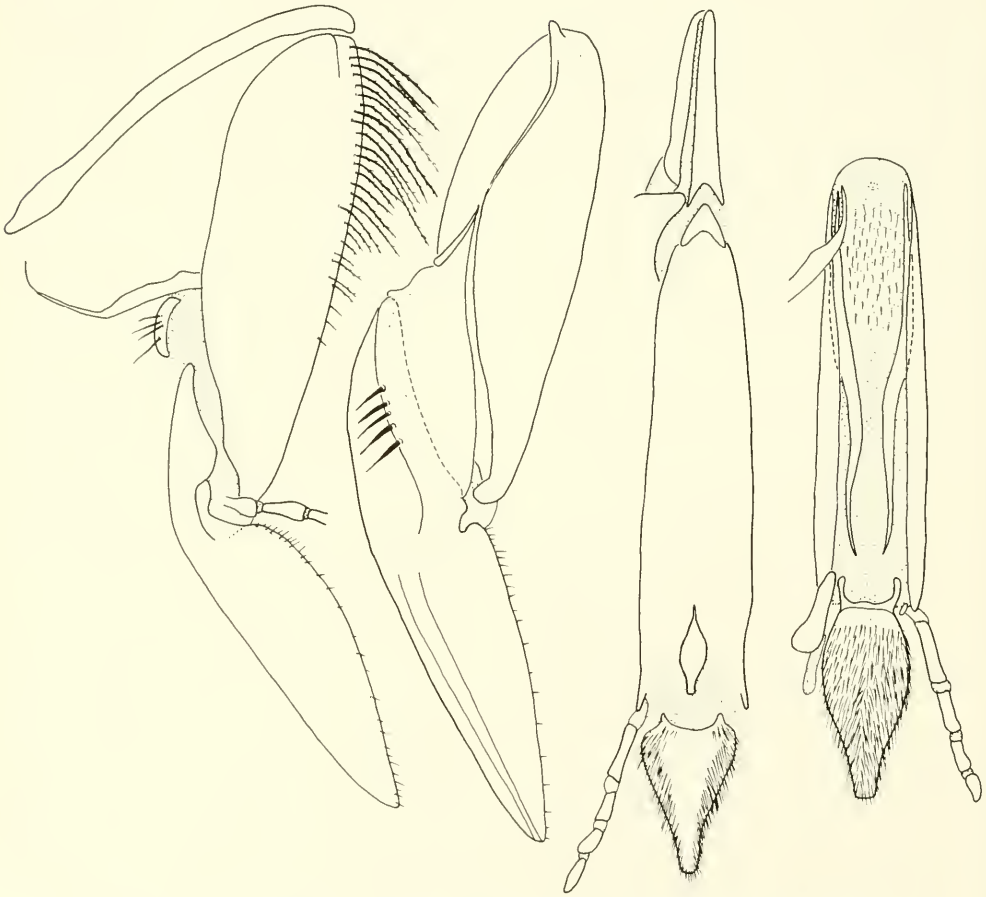


FIG. 17: Labiomaxillary complex of the short-tongued bee *Melitta leporina* (Melittidae).

comb, notched mentum, or brush on the labial palpus, all characters of some groups of long-tongued bees.

Ctenoplectra, which has been classified with the short-tongued family Melittidae, and is indeed a short-tongued bee, has been largely excluded from the above discussion since it has certain characteristics of long-tongued bees (L. Greenberg, pers. comm.). *Ctenoplectra* lacks a galeal comb, and unlike all other short-tongued bees, has a stipital comb similar to that of many long-tongued bees. Other characters common to long-tongued bees and *Ctenoplectra,* but absent in other short-tongued bees, include a flabellum, sclerotized glossal rod, and an anteriorly curved subligular process. Like other melittids, its mentum and lorum, as well as the articulation between the mentum and prementum, are like those of long-tongued bees. The length of the glossa, galea, and labial palpus of *Ctenoplectra* are similar to those of other short-tongued bees.

Long-tongued bees can be divided into two mouthpart groups, with the Megachilidae in one and Apidae, Anthophoridae, and Fideliidae in the other, here called the anthophoroid group (Fig. 18). The Megachilidae are characterized by a dististipital process (Fig. 7) (12), a thin stipital sclerite without expanded ends (Fig. 6a) (10), and a ligular arm which is not continuous with the prementum (Fig. 14); the first two characters are synapomorphous for the Megachilidae. Also, the lacinia is either curved, with a comb (Fig. 8c), or elongated, without a comb (Fig. 8f), and the stipital comb is absent in all genera except *Anthidium, Callanthidium,* and *Immanthidium* (11). In the anthophoroid group, on the other hand, the dististipital process is absent, the stipital comb is often present (Figs. 4a, d, e, f, h, i, j), the lacinia is variable, never with a comb (Figs. 8a, e), the stipital sclerite is generally expanded at one or both ends (Figs. 6b, c, e-i), and the ligular arm is fused with the prementum (Fig. 14c) (16). The last character is synapomorphous for the anthophoroid group. Since most short-tongued bees except *Melitta* and *Ctenoplectra* have fused ligular arms, this character is likely to be secondarily derived in the anthophoroid line.

Megachilidae

Within Megachilidae, Lithurginae (Fig. 23) form a distinctive group, many characters differentiating it from the other megachilids (Megachilinae and *Dioxys*) (Fig. 18, a dendrogram based on megachilid mouthparts; Table 4, a list of genera in each group). The lithurgine labial palpus has a brush at the base of the first segment, in a concavity of the inner surface, composed of long but not particularly stiff hairs (Fig. 11a) (13). The ligular arm extends nearly to the base of the prementum, adjacent to the distal end of the suspensory thickening (Fig. 14b), and is not as freely movable as the shorter ligular arm of the other megachilids (14). Also, the mentum of lithurgines is notched (Fig. 10d). Other characters uniting the Lithurginae but not unique to them include similar stipital shape (like Fig. 4g), the elongated basistipital process reaching to the lorum, short dististipital process (Fig. 7a), and similarly shaped basiglossal sclerite, paraglossal suspensorium, and paraglossa.

Dioxys (Fig. 24) is grouped with the Megachilinae because of its free ligular arm (Fig. 14a), lack of a stipital comb, and simple stipital sclerite (as Fig. 6a). However, it is unique among the megachilids in lacking the dististipital process and in having a reduced lacinia, and so is placed as a separate group. *Dioxys* also has a hairy outer surface of the stipes and a one-segmented maxillary palpus. It resembles the Megachilinae more than the Lithurginae in other characters, suggesting closer affinity with the former.

The tribes Anthidiini and Megachilini in the Megachilinae differ primarily in lacinial shape, the lacinia of anthidiines being usually curved, with a comb (Fig. 8c) (15) (except the *Stelis* group, see below). Some Megachilini, however, have the lacinia only slightly less curved, although without a comb (*Hoplitis* and *Chelostomopsis,* Fig. 8g). Other characteristics which recur in some but not all genera of both tribes include

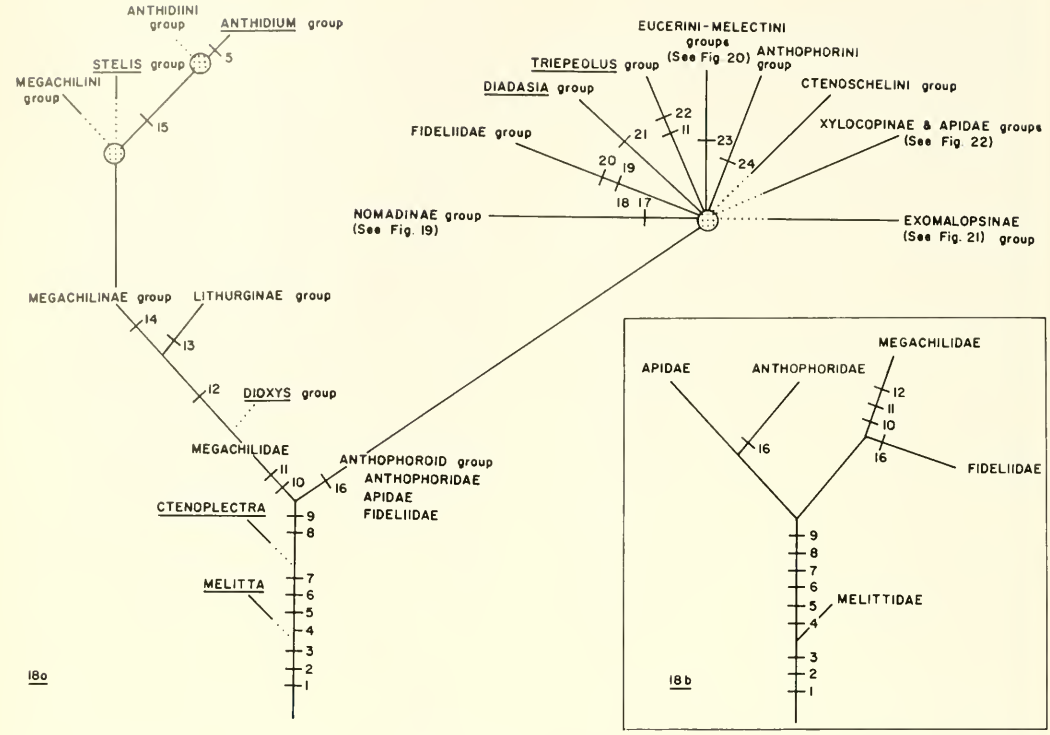


FIG. 18: a) Dendrogram showing relationships among proboscides of long-tongued bees. b) Higher classification according to Michener (1974). Dotted lines indicate groups for which there are no synapomorphic characters.

extension of the basistipital process to the lorum, plumose hairs on the stipes, long dististipital process, bifurcated mentum, similarly shaped subligular process, hairy labial palpus, and shape and relative lengths of the paraglossa and associated sclerites. While the lacinial morphology suggests divergence of the two tribes, similarities between them point to close relationship; on the basis of mouthparts alone these tribes would not be separated.

Except for the *Stelis* group and the *Anthidium* group (see below), Anthidiini are remarkably similar (Figs. 25, 26). The cardo is often widened centrally, and the stipes is generally slightly convex posteriorly, flattened anteriorly, with long bristles or plumose hairs along the posterior basal margin. The maxillary palpus is two- to three-segmented and the lacinia is curved, usually with a comb along the anterior margin (Fig. 8c). The dististipital process reaches to or almost to the stipital sclerite (Fig. 7b). The basigaleal area extends beyond the apex of the stipital sclerite (Fig. 9a). The subligular process is broad at the base, and the ligular arm, paraglossal suspensorium, and paraglossa are usually equal in length, although the length of the paraglossa may vary. The only exceptional variations among anthidiines are presence of a stipital comb in *Anthidium*, *Callanthidium*, and *Immanthidium* (Fig. 28) (structures unique to these genera among the megachilids), and lack of a lacinial comb in the *Stelis* group (Figs. 8b, 27). These genera are otherwise similar to other anthidiines, and both of these characters are likely to be secondarily derived.

The Megachilini (Fig. 29) form a fairly uniform group, without distinctive subgroups. There are no synapomorphous characters which distinguish Megachilini, nor are there such characters which might indicate the branching pattern within the megachilines. Only lacinial morphology of megachilines allows distinction from anthidiines. Generally, the maxillary palpus of megachilines has more segments (3-5) than that of

TABLE 4.

Genera Included in Each Mouthpart Group.

Dioxys Group
Dioxys
Lithurginae Group
Lithurge
Trichothurgus
Lithurgommia
Megachilini Group
Chalicodoma
Hoplitis
Chelostomopsis
Proteriades
Ashmeadiella
Creightonella
Chelostoma
Osmia
Anthocopa
Megachile
Noteriades
Anthidiini Group
Heteranthidium
Spinanthidium
Dianthidium
Paranthidium
Coelioxys
Hypanthidium
Aztecanthidium
Nananthidium
Anthidiellum
Pachyanthidium
Notanthidium
Anthidium Group
Anthidium
Callanthidium
Immanthidium
Stelis Group
Stelis
Odontostelis
Euaspis
Parevaspis
Nomadinae Group
Leiopodus
Caenoprosopis
Nomada
Holocopasites
Biastes
Fideliidae Group
Fidelia
Neofidelia
Diadasia Group
Diadasia
Melitoma
Triepeolus Group
Triepeolus
Thalestria
Eucerini Group
Thygater
Svastra
Peponapis
Eucera
Xenoglossa
Melissodes
Canephorula Group
Canephorula
Melectini Group
Melecta
Thyreus
Anthophorini Group
Anthophora
Centris
Amegilla
Epicharis
Ctenoschelini Group
Mesocheira
Ericrocis
Allodapine Group
Allodape
Braunsapis
Macrogalea
Ceratiniini Group
Ceratina
Manuelia
Xylocopini Group
Xylocopa
Lestis
Meliponinae Group
Melipona
Trigona
Hypotrigona
Meliponula
Apinae Group
Apis
Bombini Group
Bombus
Psithyrus
Euglossini Group
Euglossa
Euplusia
Eulaema
Exomalopsini Group
Exomalopsis
Ancyloscelis
Tapinotapis
Caenonomada
Tetrapedia Group
Tetrapedia

anthidiines (1-3), and the ligular arm is often slightly longer (from one to one and a half times the length of the paraglossal suspensorium), but these characters do not differentiate the two tribes. For example, there exist megachilines with two-segmented maxillary palpi (certain species of *Ashmeadiella*) and anthidiines with five-segmented maxillary palpi (*Trachusa*).

Anthophoroid group

The anthophoroid mouthpart group (families Apidae, Fideliidae, and Anthophoridae) is much more diverse at tribal and generic levels than is the Megachilidae. Certain characters are particularly useful in indicating the branching sequences throughout the group, e.g., shapes of the stipital sclerite and cardinal processes, lengths and shapes of the paraglossa and paraglossal suspensorium, and shape of the subligular process. (Figures 18 to 22 are dendrograms of the anthophoroid group, Table 4 lists genera included in each group). Justifications for branchings are given below.

The Fideliidae (Fig. 30) are distinguished by elongated outer and inner cardinal processes, that form a u-shaped articulation with the basistipital process (Fig. 3a) (19); and by the subligular process that is separated from the prementum by a membranous or lightly sclerotized area (Fig. 12a) (20). Other characteristics of the group include thickened sclerotization along the premental fold (apical to the base of the ligular area), absence of a stipital comb, plumose stipital hairs, short and narrow basistipital process, apically widened stipital sclerite, and a slightly concave apex of the mentum.

The genera of the Nomadinae (Fig. 31) (except *Thalestria* and *Triepeolus*) are united by the elongate inner cardinal process (Fig. 3c) (17), similar to that of the Fidellidae, but lack an elongated outer process. Also, the basal process of the prementum is convexly curved (Fig. 10c) (18). Within the Nomadinae, two principal subgroups are apparent, *Leiopodus, Caenoprosopis, Nomada,* and *Holcopasites,* with no stipital comb (11) and *Biastes* which has a weak stipital comb. The nomadines also have few

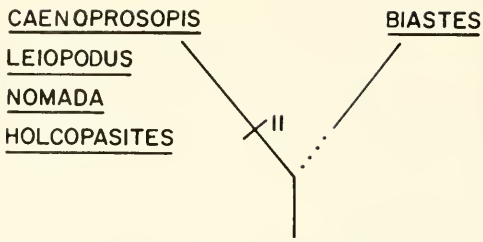


FIG. 19: Dendrogram showing relationships among proboscides of Nomadinae group. There are no synapomorphic characters shown for *Biastes*.

or no hairs on the stipes and lacinia, four- to six-segmented maxillary palpus, and a reduced stipital sclerite.

Another distinctive group is formed by anthophorid bees having an elongated paraglossae (23), the eucerines, melectines, and *Canephorula* (Fig. 20). The eucerines (Fig. 32) and *Canephorula* differ from the melectines by the length of the paraglossa (which extends to the apex of the glossa (Fig. 16c) (25), the presence of a stipital comb, and striations in the membrane underlying the lacinia (26).

The Eucerini (Fig. 32) form a homogenous group. The area between the subgalea and stipital sclerite is partly sclerotized (27), and the base of the stipes is expanded along the anterior margin (Fig. 4a). Eucerines have long, plumose hairs along the basal posterior margin of the stipes, a stipital comb, and an elongated cardo. *Canephorula* resembles the eucerines in many characters, but differs in the prementum, which is partly membranous and flattened (Fig. 12g) (28), unique among all the bees. Also, *Canephorula* has no sclerotization in the subgalea-stipital sclerite region. For these reasons, it has been placed in a separate group, but with affinity to the eucerines.

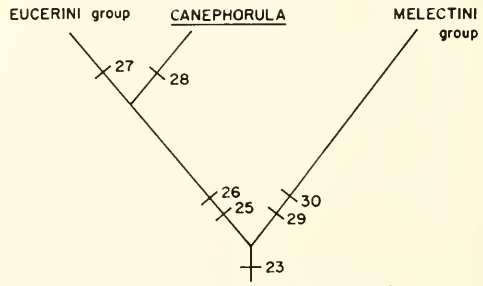


FIG. 20: Dendrogram showing relationships among proboscides of Eucerini and Melectini groups.

The melectines (Fig. 33) are characterized by paraglossae extending two-thirds of the length of the glossa (23), a brush on a small expanded lobe of the palpiger (Fig. 33) (29), a stipital sclerite which terminates basal to the basigaleal area (Fig. 9c), a convex basal premental process (Fig. 10c), and lack of a stipital comb (11). Also, there are three bristles on a membranous fold basal to the basigaleal area; the melectines are the only long-tongued bees with such setae (Fig. 9c) (30). Other characteristics of the melectines include the shape of the stipes (similar to Fig. 4g), elongated lacinia (Fig. 8f), bifurcated mentum (Fig. 10c), and broad attachment of the paraglossa to the paraglossal suspensorium (Fig. 16d). Phenetically, the melectines do not show close affinity with the Eucerini-*Canephorula;* presumably elongated paraglossa evolved separately in the two groups.

A large group is formed by the Apidae, Xylocopinae, and the Exomalopsini, Tetrapediini, Centridini, and Anthophorini of the Anthophorinae (Figs. 21, 22). While no apomorphous proboscidial characters unite all these bees, the recurrence of many characters in varied genera of this group suggests relationship among its members. These characters include the broad attachment of the paraglossa to the paraglossal suspensorium (Fig. 16a) (all except Tetrapediini and *Anthophorini* groups); the five- to six-segmented maxillary palpi (*Xylocopa, Centris, Anthophora, Caenonomada, Ceratina, Manuelia, Allodape, Braunsapis, Exomalopsini*); the presence of a stipital comb (all but the allodapines), a bipartite stipital thickening (Fig. 5c) (Xylocopini, *Manuelia,* allodapines, *Apis*); the broad, membranous or lightly sclerotized, and hairless or slightly hairy lacinia (Fig. 8e) (*Apis, Ceratina, Manuelia,* allodapines); and the long, abundant, and often plumose stipital hairs (*Centris, Anthophora, Amegilla,* Exomalopsini, Xylocopini).

The Anthophorinae most similar to the Xylocopinae-Apidae group can be differentiated into two branches, the Anthophorini group and the Exomalopsini-Tetrapediini groups (Fig. 21). The Anthophorini group (Fig. 34) differs from the latter in the unique extended apical end of the subligular process, forming a u-shaped structure upon which the glossa rests (Fig. 12f) (24). Other characteristics of the Anthophorini group include the straight and apically broadened stipital sclerite, curving anteriorly basally (Fig. 6g), the hairless or sparsely hairy lacinia, the slightly concave apex of the mentum (Fig. 10a), and the comb and plumose posterior hairs of the stipes (Fig. 4d).

Tetrapedia differs from the Exomalopsini group by the expanded apical end of the stipital sclerite (Fig. 6e), lack of a broad attachment of the paraglossa to its suspensorium (Fig. 16b), and the shape of the subligular process, narrowed apically and basally and expanded medially (Fig. 12c) (31). Exomalopsini (Fig. 35) have a broadly attached paraglossa (Fig. 16a), non-expanded stipital sclerite, a triangular subligular process (Fig. 12e), and a brush on the first segment of the labial palpus similar to that of lithurgines (Fig. 11a) (13), although not as well-developed. Also, the exomalopsines have a sclerotized ridge medially along the outer surface of the apical third of the stipes (Fig. 4j) (32); this ridge is lacking in *Tetrapedia. Caenonomada* has a unique hooked inner cardinal process (Fig. 3d).

The Xylocopinae-Apidae group (Fig. 22) is divided into three branches by differentiation of the stipital sclerite. In Xylocopini and Meliponinae, each end of the stipital sclerite is expanded into a triangular process, the larger apical process usually extending as far as the inner margin of the subgalea (Fig. 6i) (35). In the allodapines and the *Ceratina* group, the stipital sclerite is slender and slightly curved, and expanded into a small apical knob (Fig. 6d) (33). The stipital sclerite of Apidae, except Melipo-

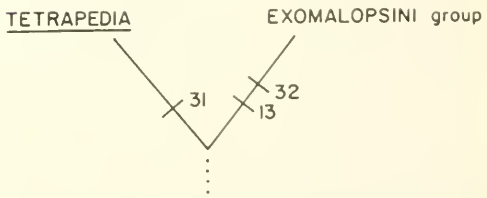


Fig. 21: Dendrogram showing relationships among proboscides of Exomalopsinae.

ninae, varies but is never like that of the other groups (Figs. 6b, c, h). The paraglossa is broadly attached to the paraglossal suspensorium in the entire group (Fig. 16a).

Ceratina (Fig. 36) and *Manuelia* differ from the allodapine bees (Fig. 37) in having a stipital comb; the allodapines are combless (11). Both groups have sparse posterior stipital hairs, a relatively short and broad basistipital process, and a broad, lightly sclerotized, hairy lacinia.

The Xylocopini-Meliponinae group is distinguished by its stipital sclerite (35), as described above, by the strongly bifurcate mentum (Fig. 10c), and by the robust anterior longitudinal brace (34). The Xylocopini (Fig. 38) form a particularly distinctive group, with heavily sclerotized maxilla, almost square stipes with a strongly curved comb indentation and extremely robust comb teeth (Fig. 4h) (36), short cardo, and bipartite stipital thickening (Fig. 5c) (37) with an expanded sclerotized area where the two parts meet. Also, the stipital sclerite is fused with the apical end of the stipital thickening, and in some species of *Xylocopa* (*X. varipuncta* and *fimbriata*) it is also fused with the stipes. Meliponinae (Fig. 39) are characterized by long, posterior bristles on the stipes (Fig. 4i), one-segmented maxillary palpus, and a long basistipital process, extending to the submentum, formed largely by the basistipital thickening (Fig. 5b) (38). *Melipona* has hairs along the posterior edge of the stipes (Fig. 39).

Apinae (*Apis,* Fig. 40) differs from Bombinae (Euglossini and Bombini) by the weak stipital comb (39), the membranous, hairless lacinia (Fig. 8e) (41), and the unique bulla on the inner cardinal process (Fig. 3f) (40). (To my knowledge, this is the first report of a stipital comb in *Apis;* this structure appears to have been overlooked by previous authors.) Bombini (Fig. 41) have a unique, strongly sclerotized ridge where the cardo diverges into the cardinal processes (Fig. 3e) (42) (not visible in Fig. 41 due to the orientation of the specimen). The stipital sclerite of the bombines is similar to that of the Meliponinae in being somewhat expanded apically, suggesting that this trait may be primitive for Apidae. Euglossini (Fig. 42) is distinguished by the extremely long glossa, labial palpus, and galea (43).

The remaining Anthophorinae form three groups, *Melitoma-Diadasia, Mesocheira-Ericrosis,* and *Thalestria-Triepeolus. Melitoma* and *Diadasia* (Fig. 43) are characterized by slight enlargement of the apical end of the stipital sclerite both anteriorly and posteriorly (Fig. 6f); a brush on the third segment of the maxillary palpus (Fig. 11b) (21); broad, membranous, and hairless lacinia (Fig. 8e); sparse plumose hairs along the entire precomb region of the stipes; and a weak stipital comb. *Melitoma* differs from *Diadasia* in having elongated glossa, labial palpus, and galea, as well as in the shape of

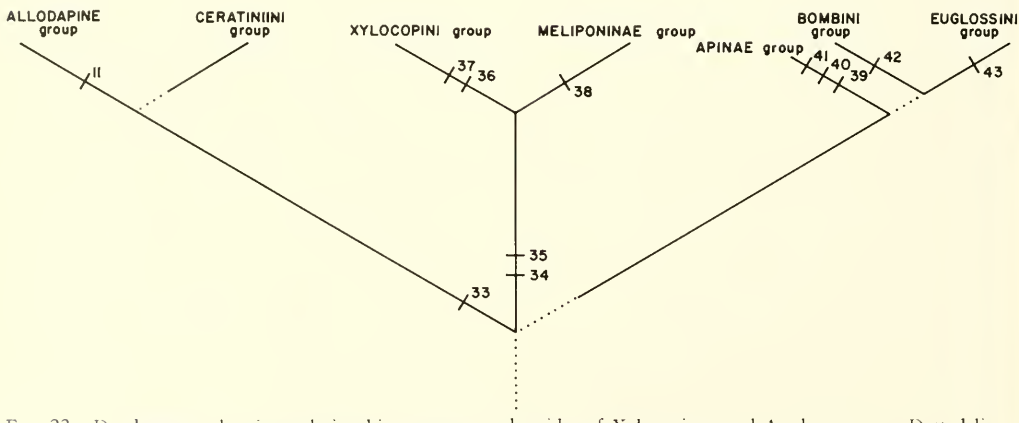


FIG. 22: Dendrogram showing relationships among proboscides of Xylocopinae and Apidae groups. Dotted lines indicate groups for which there are no synapomorphic characters.

the mentum (slightly concave apically in *Melitoma,* bifurcate in *Diadasia*).

Mesocheira (Fig. 44) and *Ericrocis* are similar in their broad lacinia, enlarged basal process of the prementum, bifurcate mentum (Fig. 10c), stipital shape (Fig. 4c), weak stipital comb, and rectangular subligular process (like Fig. 12d). For *Thalestria* and *Triepeolus* (Fig. 45), common characters include stipital shape (similar to Fig. 4g), expanded sclerotization of the junction of the stipital and basistipital thickenings (Fig. 5e) (22), broad and hairless lacinia, loss of the stipital comb (11), and a bifurcate mentum (Fig. 10c).

DISCUSSION

In the preceding sections, the comparative morphology of the proboscides of the long-tongued bees is described and a cladistic analysis of mouthpart characteristics is presented. These provide some insights into the taxonomy and phylogeny of the long-tongued bees. Instances where the present results support or disagree with current classification and phylogeny of the bees (Table 1, Michener, 1944, 1974a) will be discussed below. However, I shall not reclassify the bees; such a reclassification should be based on more characters than those of the labiomaxillary complex alone.

This study supports a monophyletic origin (Ashlock, 1971) for all long-tongued bees, the families Anthophoridae, Apidae, Fideliidae, and Megachilidae. Species in a monophyletic group must share synapomorphous characters, or unique evolutionary innovations. For long-tongued bees, such characters include the long glossa, the long and flattened first two segments of the labial palpus, the long galea, the terminal flabellum on the glossa, the internal sclerotized glossal rod (not examined for all specimens, but present in all those examined), the anterior curvature of the subligular process, the galeal midrib, the shape and articulations of the mentum and submentum, the well-developed paraglossal suspensorium, and the presence in many genera of a stipital comb. The complexity of these characters and their functional interdependence, as well as their universality among long-tongued bees, strongly suggest monophyly. Further, since there is no evidence that other groups evolved from members of this mouthpart group, it can be considered holophyletic (Ashlock, 1971).

Michener (1944, 1974a) considered Melittidae among short-tongued bees to be the closest to long-tongued bees because of the morphology of the postmentum. Melittid characters (for *Melitta* and *Ctenoplectra*) such as the form of the mentum and lorum, ligular arm similar to that of Lithurginae (Fig. 14b), and a somewhat elongated basistipital process (L. Greenberg, in prep.) are similar to those of long-tongued bees. The distinct ligular arm of *Melitta* and *Ctenoplectra* may be derived from the fused condition found in other *Melittidae,* many short-tongued bees, and the sphecoid wasps (R. McGinley, pers. comm.); fusion of the ligular arm to the prementum in the antnophorid group is thus likely to be secondarily derived. Alternatively, the anthophorid group might be primitive in this character, with *Melitta, Ctenoplectra,* and Megachilidae united by their free ligular arms. This interpretation appears unlikely, however, as it would require that the elongated glossa be evolved separately in the Megachilidae and the anthophorid gorup. The ligular arm should be re-evaluated in a study of short-tongued bees to determine the homologies of various types of fusions and separations. The short-tongued bee *Ctenoplectra,* considered to be a melittid (Michener, 1944, 1974a), is similar to long-tongued bees for most characters, excluding the length of the glossa, galea, and labial palpus. *Ctenoplectra* and long-tongued bees can be considered sister groups.

The classification of Megachilidae according to mouthpart characters generally agrees with that of Michener (1944, 1974a). Megachilidae diverge from other long-tongued bees in having a dististipital process (except for *Dioxys*) and ligular arms which do not merge with the premental fold basally, but rather rest freely in the membrane of the premental concavity (the proposed primitive

condition for long-tongued bees). Thus, their distinctiveness as a family seems justified by mouthpart characteristics. Within the Megachilidae, the Lithurginae and the Megachilinae are distinct from one another, the Megachilinae with short ligular arms and the Lithurginae with long ones and a brush on the first segment of the labial palpus, absent in Megachilinae. The tribes Megachilini and Anthidiini of Megachilinae are scarcely distinguishable; they would not have been separated on the basis of the proboscis alone.

Dioxys, previously classified either as an anthidiine (Michener, 1944) or as a separate subfamily (Popov, 1947), differs from anthidiines in important labiomaxillary characters, such as reduced lacinia and lack of a dististipital process. Non-mouthpart characters (reduced sting, absence of a scopa) support placement of *Dioxys* in a separate group, possibly as a tribe of Megachilinae. *Coelioxys* (in Megachilini according to Michener, 1944) has an anthidiine-like lacinia and lacinial comb, as well as a scutellum separated into dorsal and posterior surfaces by a distinct angle, an anthidiine characteristic (Michener, 1944); re-examination of its taxonomic position may also be warranted. *Anthidium, Immanthidium,* and *Callanthidium* are unique among Megachilidae in having stipital combs, probably a convergent feature rather than a synapomorphous character uniting these genera with other groups possessing stipital combs. Independent origin of the stipital comb in this group is suggested by the lack of such a comb among all other megachilids, the irregular occurrence of the comb in members of the anthophorid mouthpart group, and the similarity of *Anthidium,* etc., to the other Anthidiini in other mouthpart characters.

Of some interest is the placing of Fideliidae with the anthophoroid group rather than Megachilidae, where it is placed by Rozen (1970, 1977) (Figs. 18a, b). While fideliid larvae show similarities to those of megachilids, the fusion of the ligular arm with the premental fold (a synapomorphous character for the anthophoroid line) as well as non-mouthpart characters (mandibular structure, independent volsellae, and wing venation, Michener, 1944) support recognition of the Fideliidae as a separate family. However, the extended region of sclerotization along the premental fold apical to the point where the ligular arm merges with it in Fideliidae (Fig. 30) may be homologous with the extended base of the ligular arm characteristic of Lithurginae (Fig. 14b). If so, Fideliidae might be grouped with the Lithurginae, but this grouping would require independent origin of the fused ligular arm in Fideliidae and the anthophoroid group.

A close relationship between the Meliponinae and the Xylocopinae is indicated by mouthparts (Winston and Michener, 1977). While non-mouthpart characters (such as presence of a corbicula) support the inclusion of the Meliponinae in the Apidae, the mouthpart similarities of this subfamily to the Xylocopini suggest early divergence of the Meliponinae from the other apids.

Some affinities appear, on the basis of similarities recurring in some but not all genera, between the Xylocopinae and certain tribes of Anthophorinae (Exomalopsini, Tetrapediini, Centridini, and Anthophorini). More and better (i.e., synapomorphous) characters would be needed to justify recognition of such a group; however, it may be that these tribes of Anthophorinae share a common ancestor with the Xylocopinae. Within the Xylocopinae, the allodapine bees stand out as a group distinct from the Ceratini and Xylocopini. The allodapines have not been considered as a taxon (Michener, 1974a); if other characters support their distinctiveness, they should be considered as a separate tribe (Allodapini) of the Xylocopinae.

On the basis of similarities in mandibular structure, Michener and Fraser (1978) have suggested that the Xylocopinae and Lithurginae (Megachilidae) may be related. The structures of the labiomaxillary complexes do not support this idea; both are among the most distinctive of the mouthpart groups. Mandibular similarities between Xylocopinae and Lithurginae thus appear to reflect convergent evolution, presumably related to their wood-nesting habits.

Triepeolus and *Thalestria,* both Nomadinae according to Michener (1944) and others, are not included in the Nomadinae mouthpart group. Their distinctive mouthparts suggest that these genera may not be closely related to other Nomadinae.

The position of *Canephorula* as a sister-group to the Eucerini was suggested by Michener (1944). Although in that classification it was included in Eucerini, *Canephorula* was separated into a tribe of its own by Michener et al. (1955). The present study supports placing *Canephorula* in a sister tribe (*Canephorulini*) to Eucerini on the basis of synapomorphous characters of the two groups. The placement of *Thyreus* and *Melecta,* on the basis of mouthparts, as a sister group of the Eucerini and Canephorulini is not supported by other characters (Michener, 1944). Although these groups have what could be considered as a synapomorphous character, the elongated paraglossa, they are otherwise extremely distinct. The elongated paraglossa appears to be convergent rather than synapomorphous.

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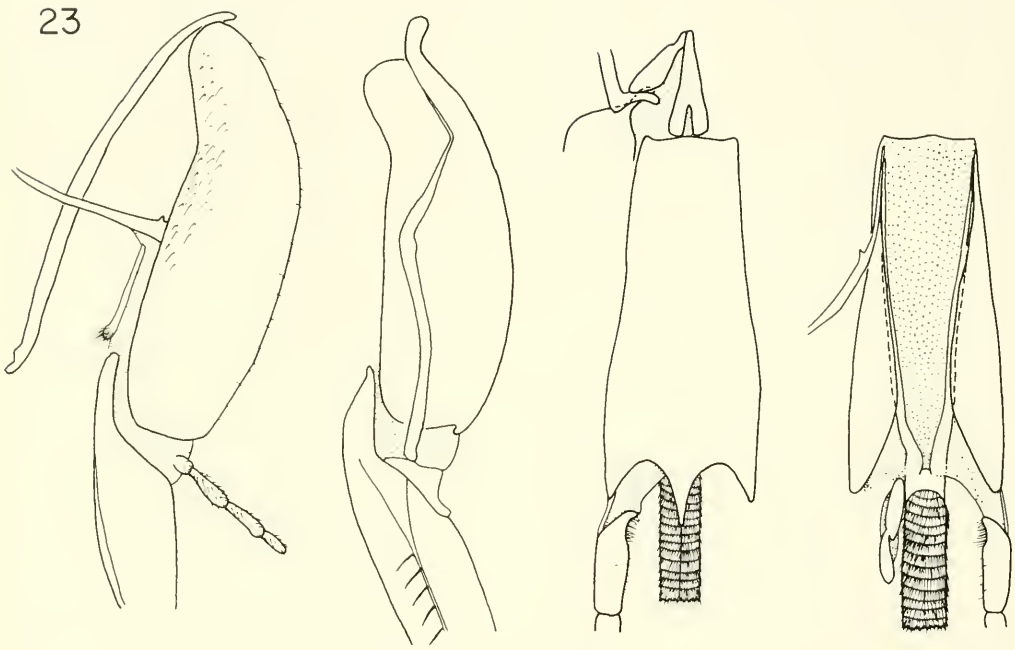
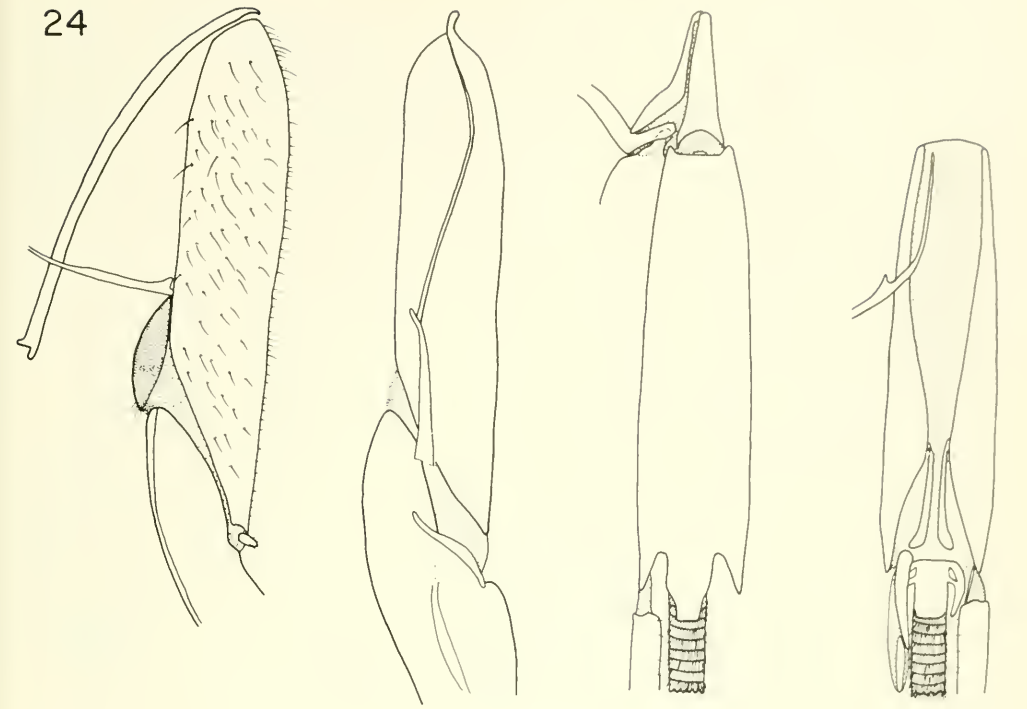


FIG. 23: *Lithurge gibbosus*.



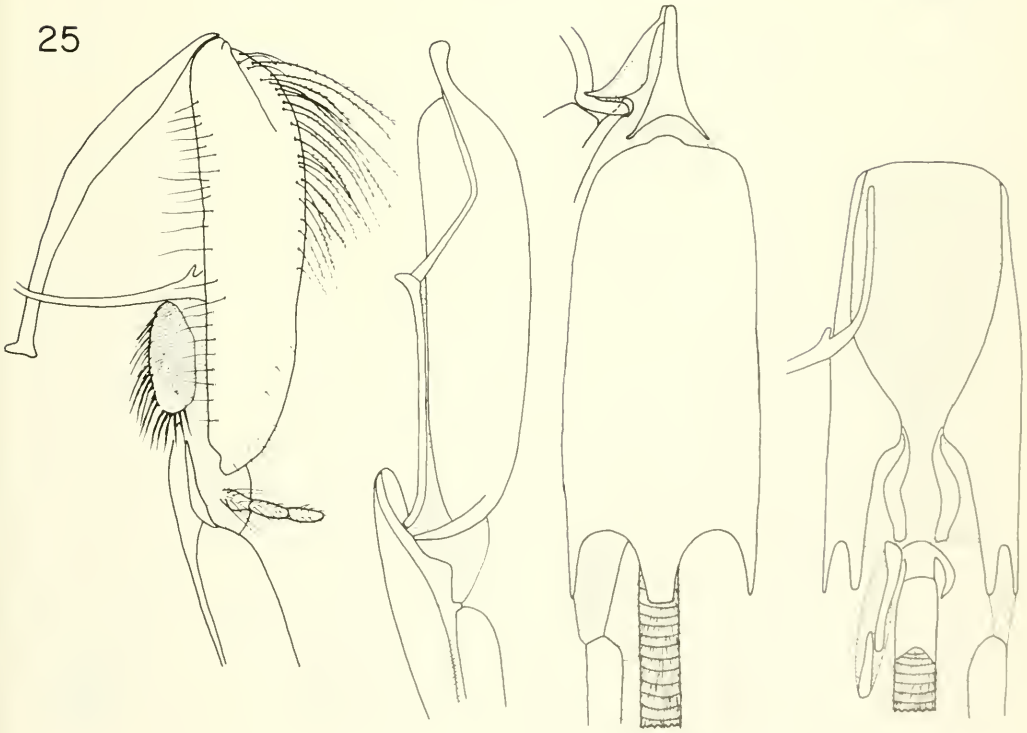


Fig. 24: *Dioxys productus subruber.*
Fig. 25: *Heteranthidium bequaerti.*

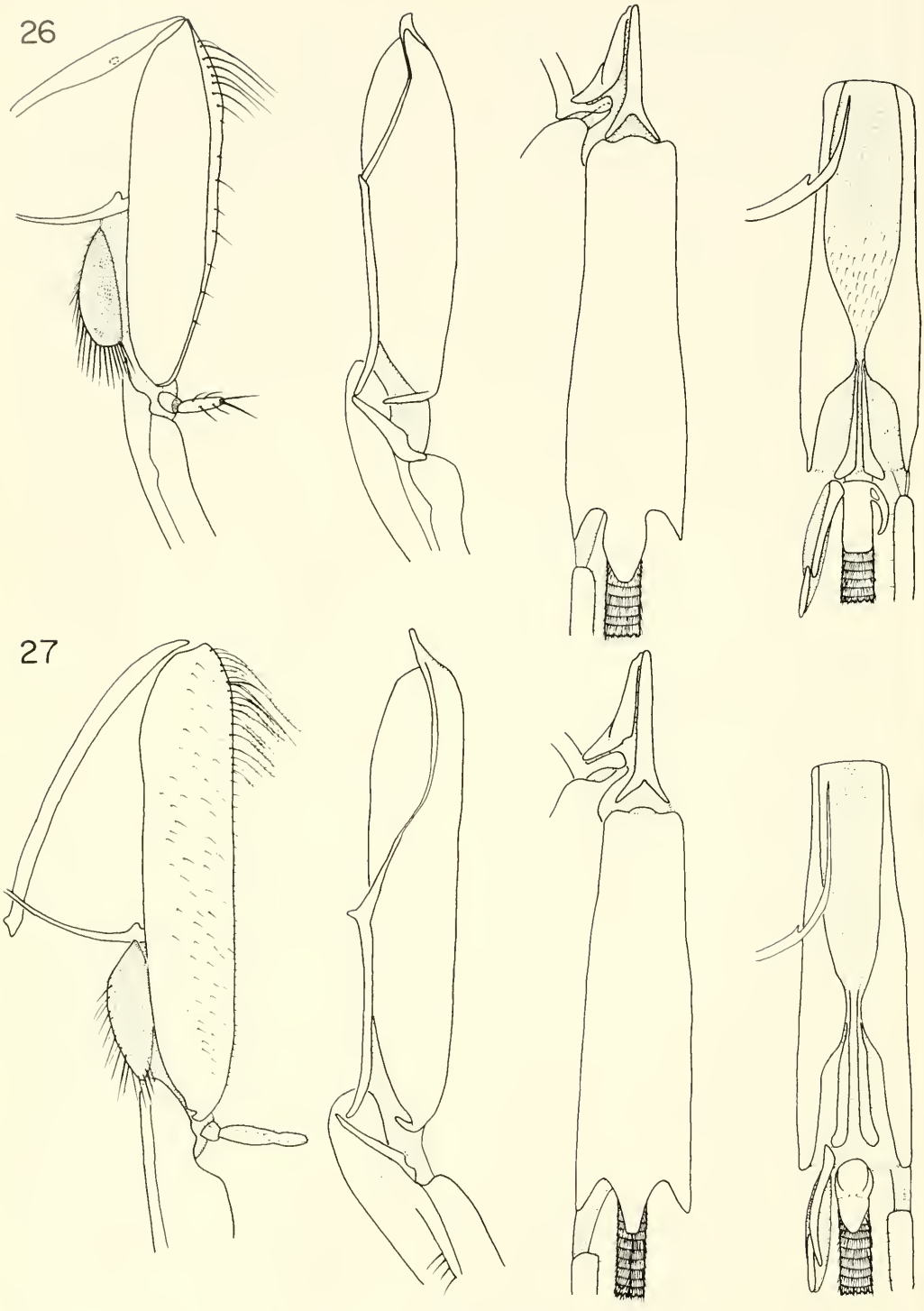


FIG. 26: *Hypanthidium taboganum.*
FIG. 27: *Stelis atterima.*

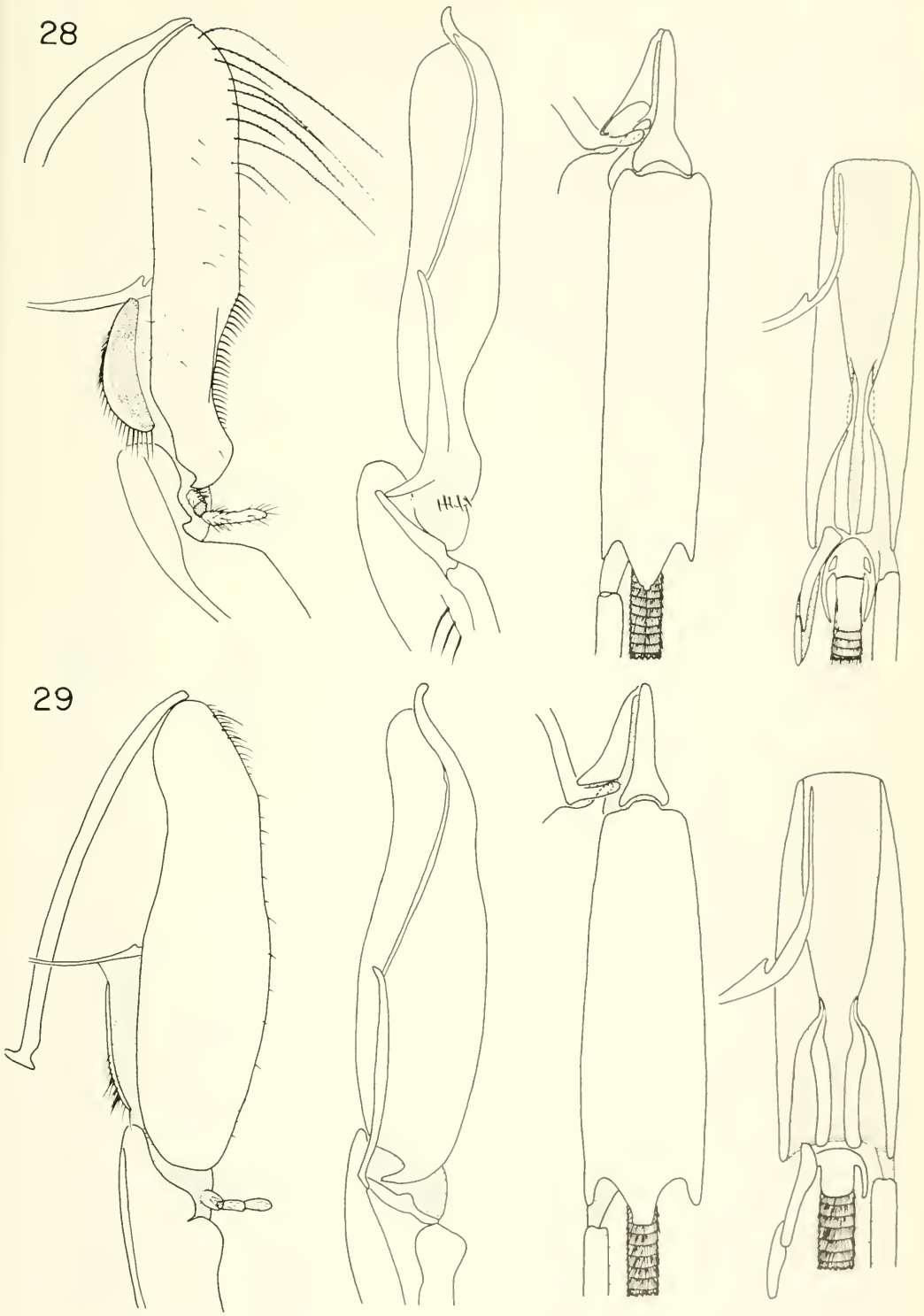


FIG. 28: *Anthidium manicatum.*
FIG. 29: *Megachile albitarsis.*

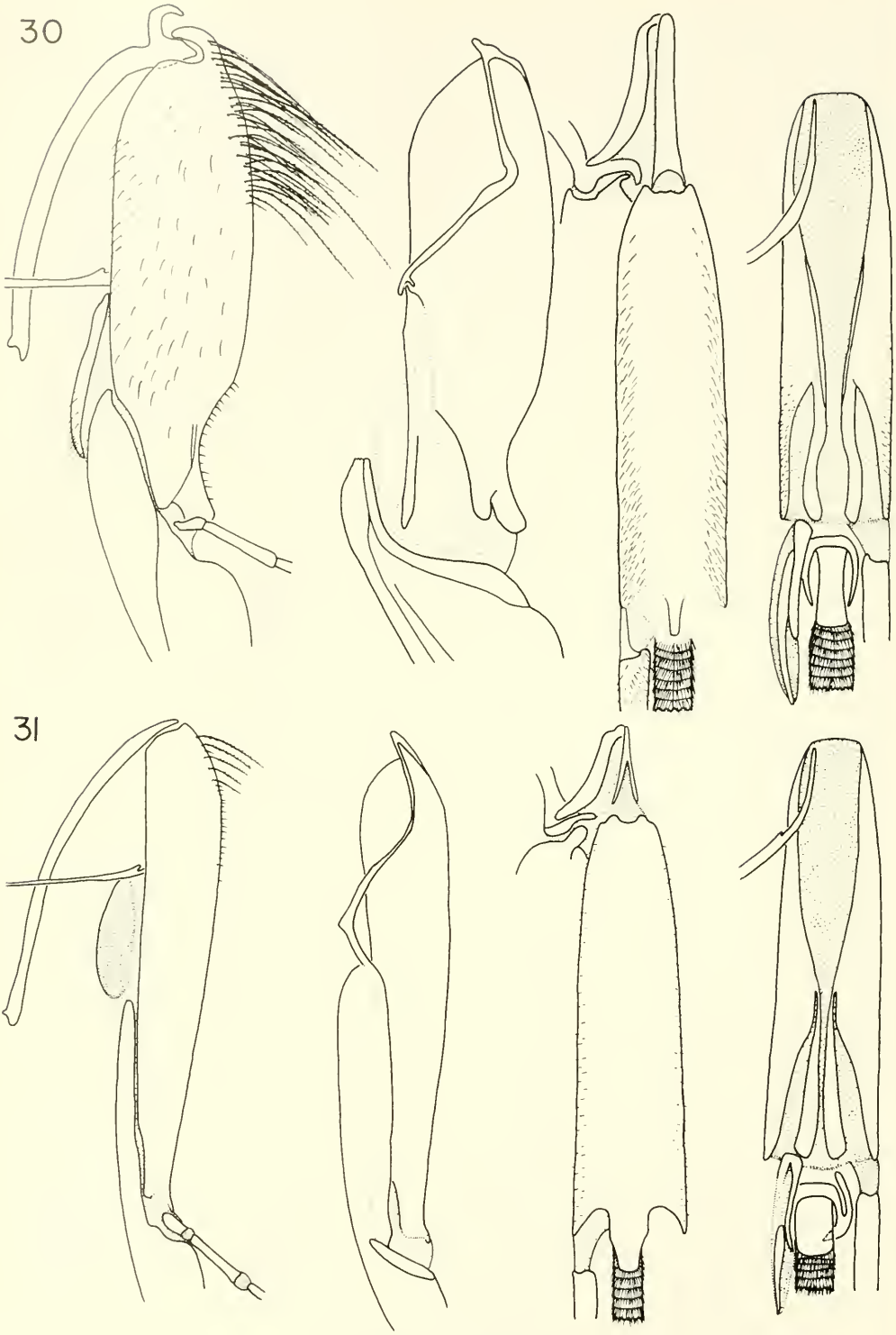


FIG. 30: *Neofidelia profuga.*
FIG. 31: *Nomada annulata.*

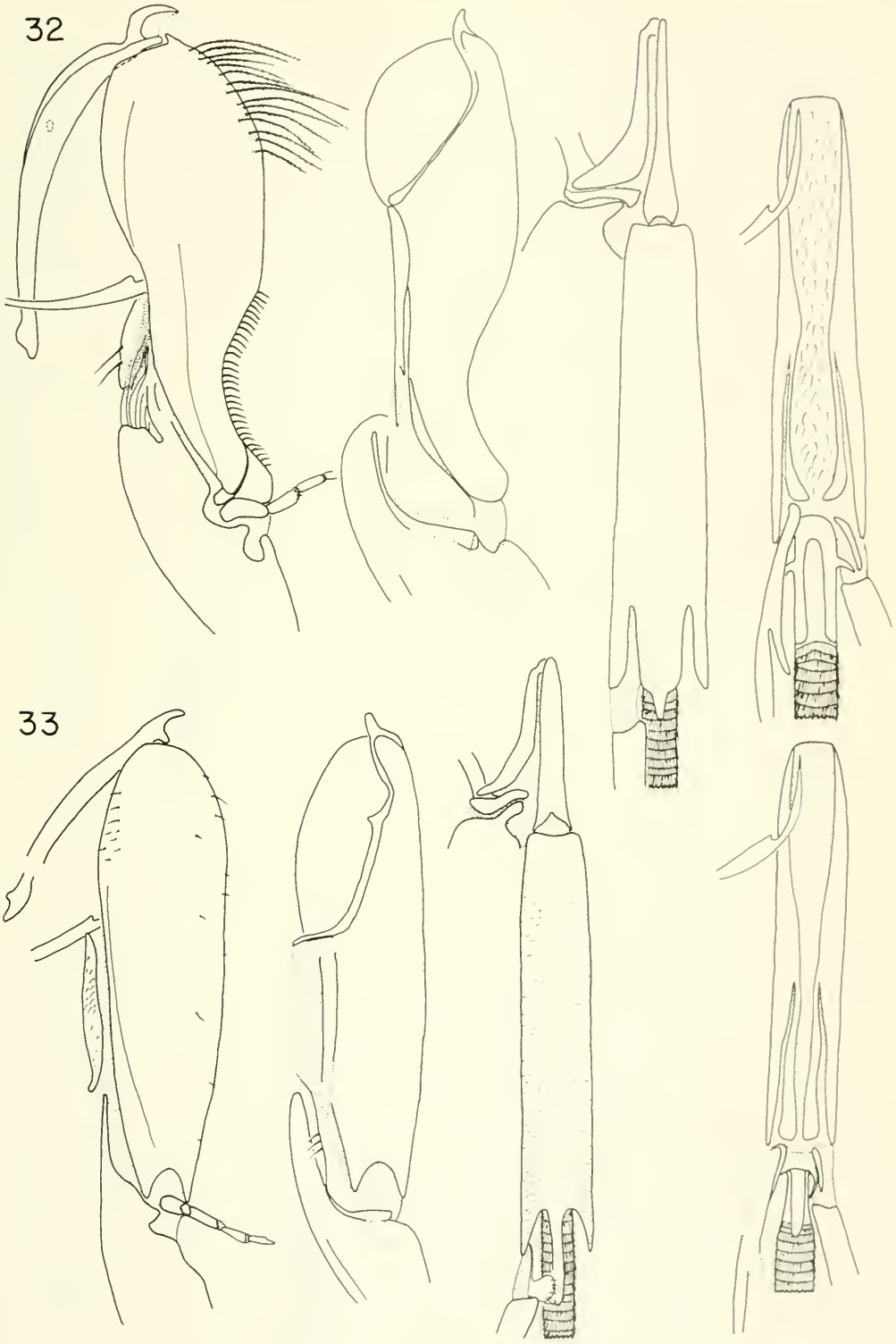


FIG. 32: *Eucera chrysopyga.*
FIG. 33: *Melecta californica.*

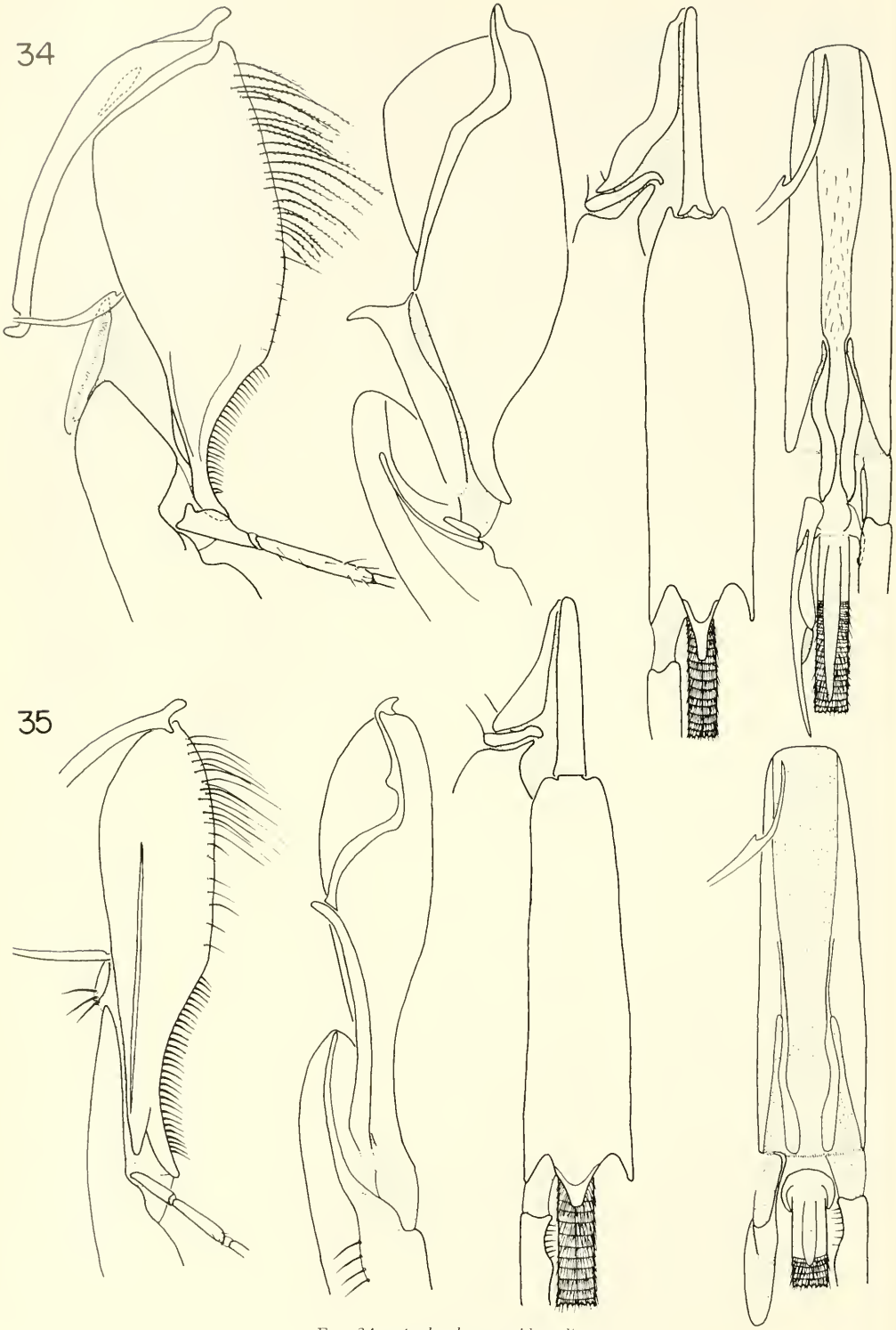


FIG. 34: *Anthophora occidentalis.*
FIG. 35: *Exomalopsis zexmeniae.*

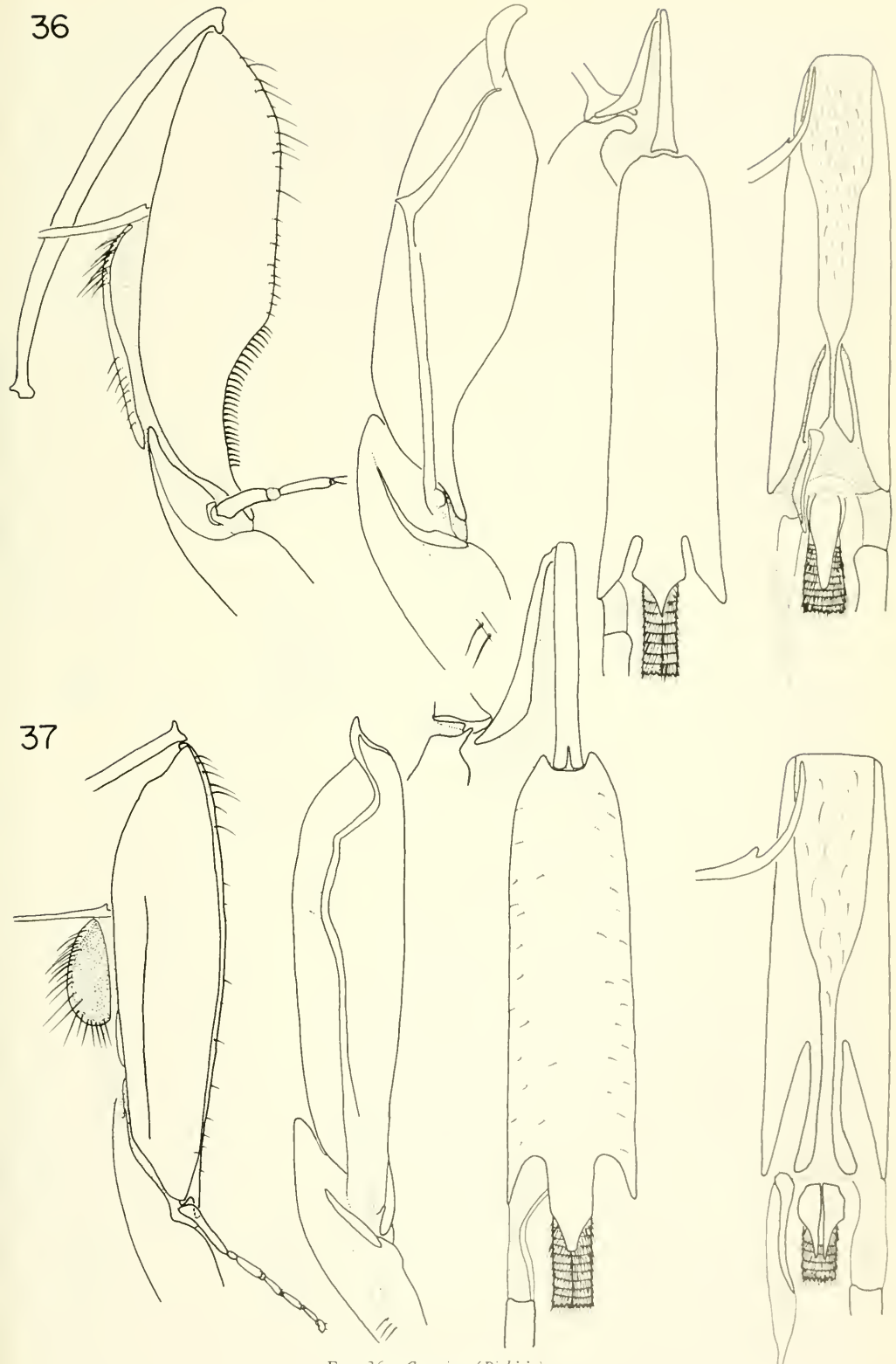


FIG. 36: *Ceratina (Pithitis)* sp.
FIG. 37: *Allodape stellarum*.

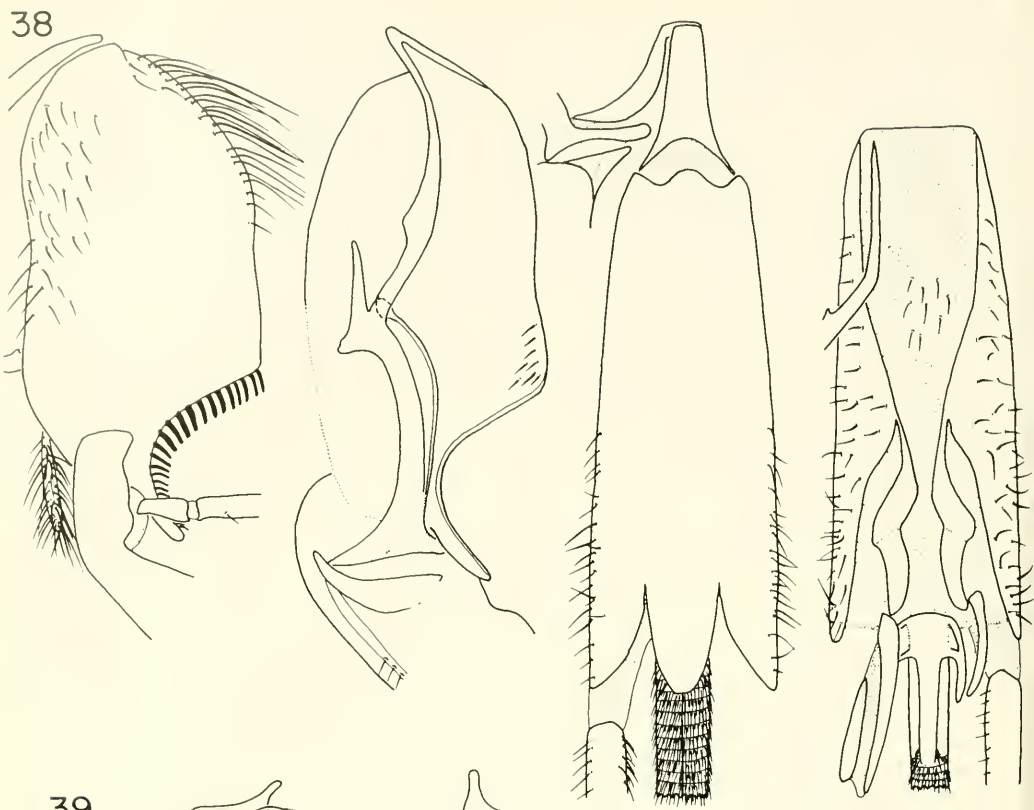


FIG. 38: *Xylocopa virginica.*
FIG. 39: *Melipona fasciata.*

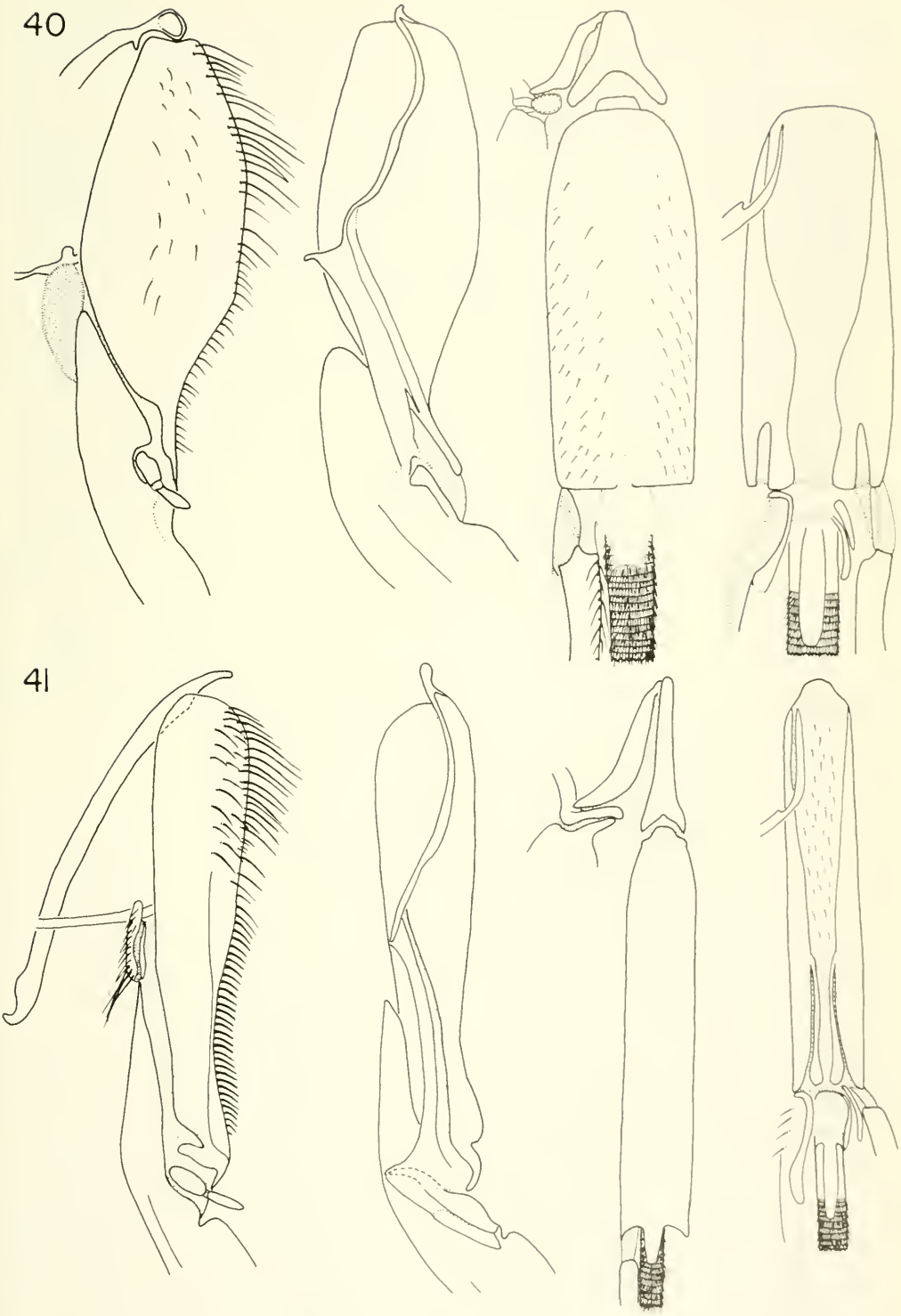


FIG. 40: *Apis mellifera.*
FIG. 41: *Bombus americanorum.*

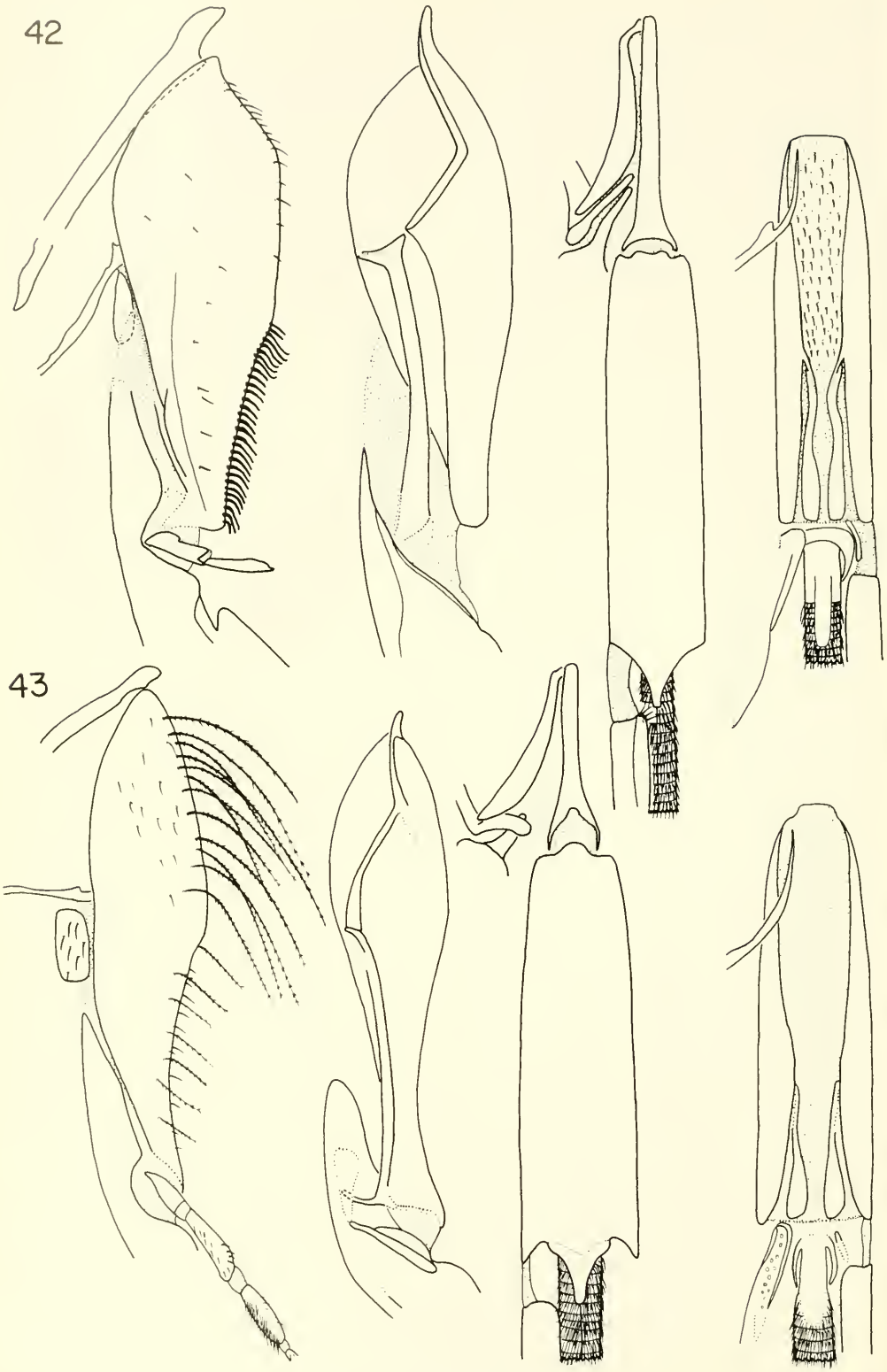


FIG. 42: *Euplusia violacea.*
FIG. 43: *Diadasia afflicta.*

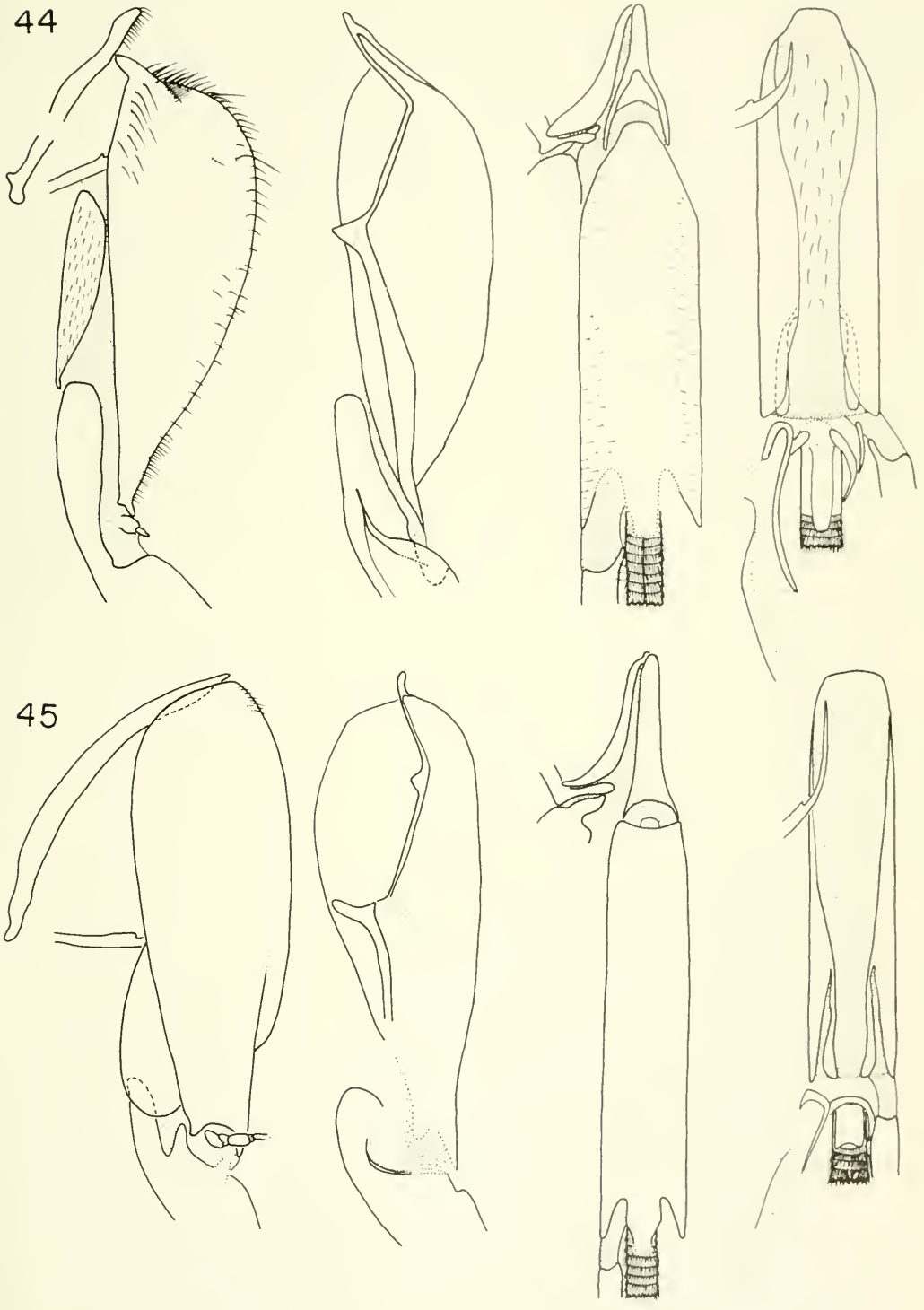


FIG. 44: *Mesocheira bicolor.*
FIG. 45: *Triepeolus verbesinae.*

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Some Effects of Adenosine Triphosphate on Swimming and Photophobic Response of *Euglena gracilis*

By
MERCEDES L. ACUNA
and
EUGENE C. BOVEE

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Some Effects of Adenosine Triphosphate on Swimming And Photophobic Response of *Euglena gracilis**

Mercedes L. Acuña[1] and Eugene C. Bovee[2]

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ABSTRACT

The potassium salt of adenosine triphosphate (K_2ATP) affects both swimming rate and photophobic response of *Euglena gracilis*. Concentrations more than 1×10^{-4} molar depressed and stopped swimming rate; 1×10^{-4} M and 1×10^{-5} M accelerated it, the latter to more than 200% more than normal rate. Pulsing rate of the flagellum (beats begun per second) as evidenced by high speed cinematography (125 and 200 frames per second) showed stoppage in 15 min in 1×10^{-2} M ATP; decrease to about 50% of normal, continued through 30 min in 1×10^{-3} M ATP; but increase to 80% above normal, rising to 145% above normal in 30 min in 1×10^{-4} M; and increasing at once to 98% above normal and rising to more than 200% above normal in 30 min in 1×10^{-5} M. Euglenas untreated with ATP do not react on entering a brighter spot of light, but swerve to a new path on leaving it. Euglenas treated with 1×10^{-4} M ATP violently whirl the flagellum, pivoting rapidly on entering the brighter spot of light, then contract violently and become temporarily immobile on leaving it. These results confirm that available ATP regulates the rates of flagellar beating and swimming and, also, that *Euglena* has two responses to light, i.e., to a sudden increase and to a sudden decrease above or below a critical threshold of intensity.

INTRODUCTION

Little research has been devoted to the effects of chemicals on swimming and phototaxis of *Euglena,* despite a plethora of research on its biochemistry and on the effects of pharmacological and other chemicals on its growth and metabolism (see 2 volumes, Buetow, 1968). *E. gracilis* grown at pH 6.8 swam most rapidly at pH 5.8 and nearly as fast at pH 7.0 (Lee, 1954) and tends to swim toward a region of acid pH (Bowne & Bowne,

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1967) or to congregate where the pH is near 6.0 (Borgers & Kitching, 1956). Some chemicals which, when present in certain concentrations, inhibit or stop swimming of *Euglena* include $NaCl_2$ and $CaCl_2$ (Schröder, 1927), acetate (Danforth, 1953; Bates & Hurlbert, 1970), glucose (Hofler & Hofler, 1952), heavy metal salts (Jirovec, 1935), arsenic (Rubinsky & Zrynkina, 1935), deuterium (D_2O) (Mandeville, et al., 1964), the 5-isomer of parathion (Lazaroff, 1968), antibiotics (Goodwin, 1951), dodecyl sodium sulfate (Galdiero & Rossano, 1966), or excesses of gasses, e.g., N, CO_2, or O_2 (Kostir, 1952). A lack of Mg^{2+} in the medium, or of certain trace-cations, causes immobilization of *Euglena gracilis* (Wolken, 1967). Certain specific metabolic inhibitors also reduce or stop swimming, e.g., 2,4-dinitrophenol below pH 6.5 (Mikolajczyk, 1969), iodoacetate (Danforth & Erve, 1964), urethan and sulfonomid singly or together (Jira & Ottova, 1950), dichlorphenol, indophenol, or salicylaldoxime (Diehn & Tollin, 1967).

Reported inhibitors of the phototactic response of *Euglena gracilis* include deuterium (Pittendrigh, 1960), and various metabolic inhibitors (Diehn & Tollin, 1967). Anything that reduces motion also reduces phototactic response (Jahn & Bovee, 1968).

Adenosine triphosphate has been indicated as the principal energy reservoir for both swimming and phototactic movements (Diehn & Tollin, 1967; Wolken, 1967; Jahn & Bovee, 1968) and glycerinated flagella of *Euglena gracilis* are reactivated and swim in ATP solutions (Mahenda, et al., 1967). Diehn (1969a, 1970) suggests that available ATP levels may alter the critical levels of light-energy needed to cause the motile response by *Euglena*. In "normal" circumstances (i.e., standard culture medium) a change of intensity from 0.2 kW/m^2 to 0.1 mW/m^2 produces a positive phototaxis (Diehn, 1969b). A change from 0.2 kW/m^2 to 0.5 kW/m^2 causes a photophobic response. (Diehn, et al., 1975). Alignment perpendicular to a plane of polarized light occurs at ~ 0.2 kW/m^2 (Creutz and Diehn, 1976).

However, except for our preliminary report (Bovee, et al., 1969; Bovee & Acuña, 1970), no one else appears to have reported the effects of ATP in solution in the surrounding medium on the swimming rate of *Euglena*, or on its responses to light.

MATERIALS AND METHODS

A green strain of *Euglena gracilis* obtained from the Carolina Biological Supply Co. was grown axenically in Chalkley's solution (Chalkley, 1930) with a few drops of added proteose-peptone solution (Neff, 1959).

Before observing normal swimming, one ml of *Euglena* culture was mixed in 5 ml of Chalkley's solution and buffered with KOH to pH 7.0. The euglenas were allowed to adapt for 30 minutes.

Swimming rate was then timed electrically to nearest 1/10 sec over a linear course (the length of a calibrated ocular micrometer scale) while observed microscopically at 20× and rate was calculated as μm/sec. Three timings were made for each of 12 organisms and averaged normal rate determined. The already tested sample was then mixed with K_2ATP dissolved in Chalkley's solution and buffered at pH 7.0 with KOH so that the resulting ATP concentration was either 1×10^{-2} M, 1×10^{-3} M, 1×10^{-4} M. Swimming was timed after exposures to ATP for 1, 10, 20, or 30 min and at each of 1, 2, 3, 4, 5, 6 and 24 hrs. At least 3 rate-calculations were made for each of 12 organisms at each interval of exposure to ATP, and average rates determined.

To make a permanent record of locomotory and photophobic responses, motion pictures were taken through a Zeiss-Nomarski phase-contrast-interference microscope at 160×, with illumination by a 60-watt incandescent lamp built into the base of the microscope. Light-intensity was controlled *via* a Zeiss Regel transformer. The motion pictures were taken with a Locam 16-mm high-speed camera (Model 164-4, Red Lake Labs) mounted at the photo tube of the microscope. Cinematographic speed was 125 pictures/sec for normal swimming, and 200 p/s for ATP-influenced swimming. Five-second sequences of film (1,000 frames each) were cinephotographed of *Euglena* immediately after immersion in ATP solution, and after 1, 5, 10, 15, and 30 minutes of immersion. Eastman Kodak tri-X 449 reversal film (type 7278 in 100 ft rolls) was used, then professionally developed.

The film was projected and analyzed with an electronically controlled Bell and Howell reversible 16-mm projector adapted for variable speed (1-24 p/s) and stop-motion analysis, equipped with a reversible frame counter ("Selectra-frame" Model 16N by TRAID Corporation, Glendale, California).

Drawings were made by tracing with india ink on clear acetate sheeting taped on glass over a film editor, model S.O.S. (Photo-Cine-Optics, Inc.). Enlargements of tracings were made by proportional transfer to ruled graph paper.

Photographic prints were made from the cinefilm with standard photographic enlarger on high contrast photographic paper, using standard photographic darkroom techniques.

OBSERVATIONS AND RESULTS

Forward Swimming

Normal rate of swimming for *Euglena gracilis* in Chalkley's solution at pH 7.0 ranged from 139 to 145 μm/sec, with an average normal rate of 142 μm/sec.

Effects of ATP on Forward Swimming

The first response of *Euglena* to addition of the K_2ATP solutions is the classic "shock reaction" (Jennings, 1906), normal forward swimming being replaced for a few seconds by a pivoting movement.

In K_2ATP at 1×10^{-2} M, swimming stopped within 15 min and euglenoid movement stopped a few seconds later. No movement was observed for 12 hrs, but normal movement was recovered overnight, sometime after 12 hrs exposure and within 24 hrs in the solution. In 1×10^{-3} M ATP more than 90% of the euglenas slowed 50% in forward progress almost immediately, contracted to globular form after 6 hrs and remained inactive for 12 hrs. Sometime within the next 24 hrs, normal motility and swimming rate were regained. In 1×10^{-4} M ATP a brief, pivoting, shock-reaction was followed by an increase in locomotor rate within 10 min to 13% above normal (160 μm/sec) and then declined almost to normal after 30 min in ATP (144 μm/sec), then again increased within one hr of exposure to 38% faster than normal (196 μm/sec) and continued to accelerate during a 24 hr period, being then 99% faster than normal (282 μm/sec). In 1×10^{-5} M ATP the swimming rate rapidly increased within the second and third hrs of exposure to 80% faster than normal (259 μm/sec), declined in rate within a total of 6 hrs exposure to 51.3% faster than normal, and within a total of 24 hrs exposure returned to normal or slightly subnormal swimming rate. These data are summarized in Figs. 1 & 2.

Effects of ATP on the Pulsing Rate of the Flagellum

Analysis of motion pictures taken of normal swimming at 125 f/s and of ATP-influenced swimming at 200 f/s showed

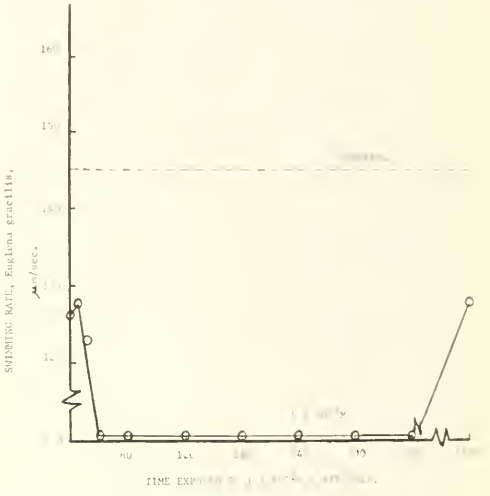

Fig. 1. Effect of 1×10^{-2} M ATP on swimming rate of *Euglena gracilis*.

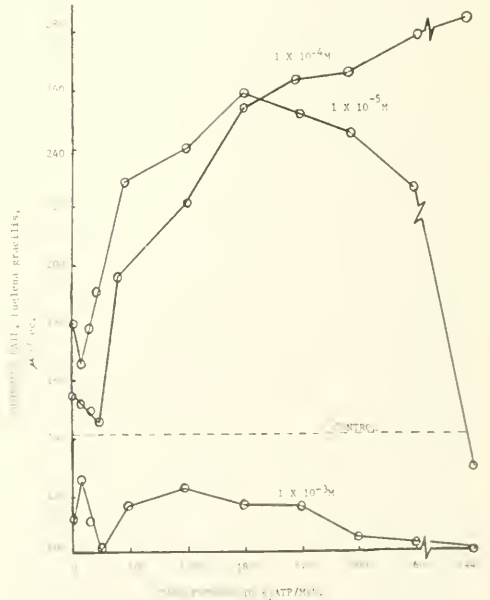

Fig. 2. Effects of 1×10^{-3} M, 1×10^{-4} M and 1×10^{-5} M ATP on the swimming rate of *Euglena gracilis*.

that the number of helical-waves/sec progressing along the flagellum was altered by exposure to ATP in the surrounding solution.

Normal pulsing rate of the flagellum of *E. gracilis* under the conditions of cinephotography varied from 20 to 22 pulses/sec, i.e., one each 45-50 msec, nearly twice the pulsing similarly recorded for *E. viridis* (Lowndes, 1944; Holwill, 1965).

In 1×10^{-2} M K_2ATP, flagellar beating was erratic and the number of waves/sec was much less than normal, failing to propel the body at all after 20 min exposure. In 1×10^{-3} M ATP, flagellar pulsing was less erratic and the number of waves/sec was 40-50% fewer than normal (9-11/sec). However, in 1×10^{-4} M and 1×10^{-5} M flagellar pulsing was steady and the number of waves/sec *increased* in 1×10^{-5} M ATP from the average of 20/sec (one each 45-50 msec) to a maximum of at least 65/sec, i.e., one each 14-15 msec, a trebling of the pulsing rate in 30 min. The increase in frequency of wave-origin was coincident with similarly greater rate of progress of the helical waves along the flagellum, and not with an increase in the number of waves seen serially progressing along the flagellum at any one time. As in normal swimming, there were no more than 2 waves in progress at any one time.

The increase in pulsing rate was almost immediate, in 1×10^{-5} M K_2ATP rising to about 47/sec (one each 20-22 msec) in less than one minute, a more than doubling of rate. The rate of pulsing continued to increase, with slight fluctuation, to the maximal rate (65/sec) after 30 min eposure to 1×10^{-5} M K_2ATP (Fig. 3).

PHOTOPHOBIC RESPONSE

Euglenas observed directly by phase-contrast microscopy adapted quickly in Chalkley's solution to the light-intensity

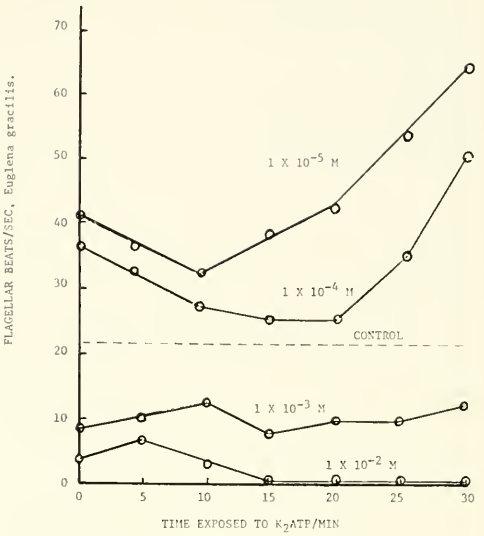

FIG. 3. Effects of several concentrations of ATP on the number of flagellar beats per second by *Euglena gracilis*.

of the microscopic field, swimming through it with no photophobic reaction. However, when the phase-condenser was adjusted so that a slightly, visibly-brighter spot of light 15 to 35 μm diameter was concentrated in the center of the field, the euglenas swerved at an angle of 45° to 60° to right or left of the linear path of swimming on going out of the spot of light. The reaction was an off-response occurring as the anterior end of the euglena left the brighter area, and was completed in 0.65 sec (Fig. 4). Each euglena immediately resumed normal swimming along the new line of direction while still in the generally lighted microscopical field.

Effects of ATP on Photophobic Response

In K_2ATP solution 1×10^{-4} M, the same euglenas earlier observed in Chalkley's solution, alone, showed in less than one minute an intense photophobic response to the same spot of light, although they swam normally in the generally lighted area of the microscopical field.

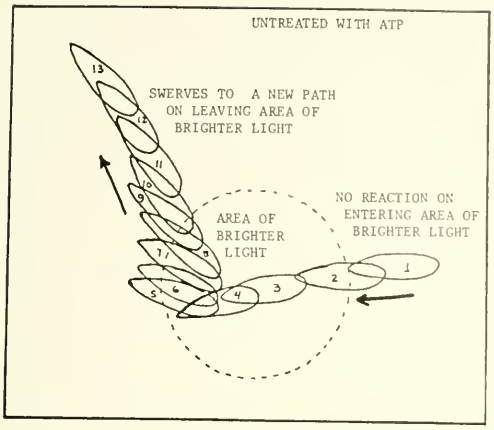

Fig. 4. Path of *Euglena gracilis* untreated with ATP on entering and leaving a brighter spot of light. Traced from a motion picture film photographed at 125 frames per second. Each 15th picture in a 200 frame sequence is shown.

This response was initially an on-response, beginning before the anterior end of the body had passed through the brighter spot. The flagellum was thrown to the side or forward with undulations increasing in amplitude, rate, and thrust so that a vortex of water was created around the flagellum (Fig. 5). The vortex obscured the undulations so that the exact increase of pulsing rate could not then be calculated.

This rapid, anterior, flagellar pulsing caused the euglena to pivot rapidly on the fringe of the brighter spot, describing 3 complete turns in 0.35 sec (one complete turn per 117 msec). Within the following 0.5 sec the euglena, still pivoting, pulled itself forward out of the bright spot. It then contracted to nearly globular form as an off-response on leaving the bright spot and forward swimming was suspended. The pivoting, contraction and cessation of forward swimming occurred within 1.025 sec (Fig. 6). After several minutes these contracted euglenas relaxed, extended and began normal locomotion which increased in rate until it exceeded the normal rate in Chalkley's solution.

This violent photophobic response occurred at any time during the first half-hour of exposure to 1×10^{-4} M K_2ATP and whenever a euglena entered the brighter spot of light, as evidenced by cinephotography. It also was observed visually at any time during 24 hrs exposure to 1×10^{-4} M K_2ATP on increasing the light slightly by moving the rheostatic control of the Regel transformer. Attempts to measure the increase of intensity required to elicit the reaction were inconclusive due to inadequate sensitivity of equipment available. However, the requisite change of intensity needed to cause a phototactic or photophobic response may be minimal (Diehn, 1969), so long as it exceeds a critical intensity.

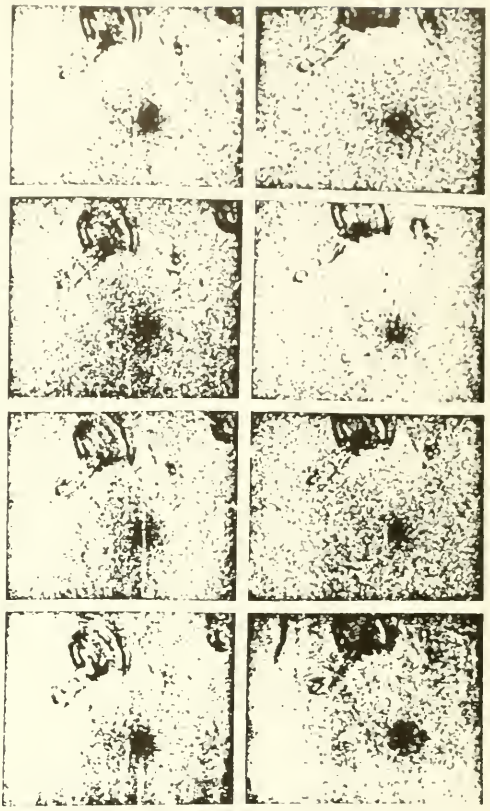

Fig. 5. Eight consecutive pictures from a motion picture taken at 200 frames per second showing the initial reaction of *Euglena gracilis*, treated with 1×10^{-4} M ATP, on entering a brighter spot of light. The vortex in the water created by rapid whirling of the flagellum at the upper end of the cell is clearly shown.

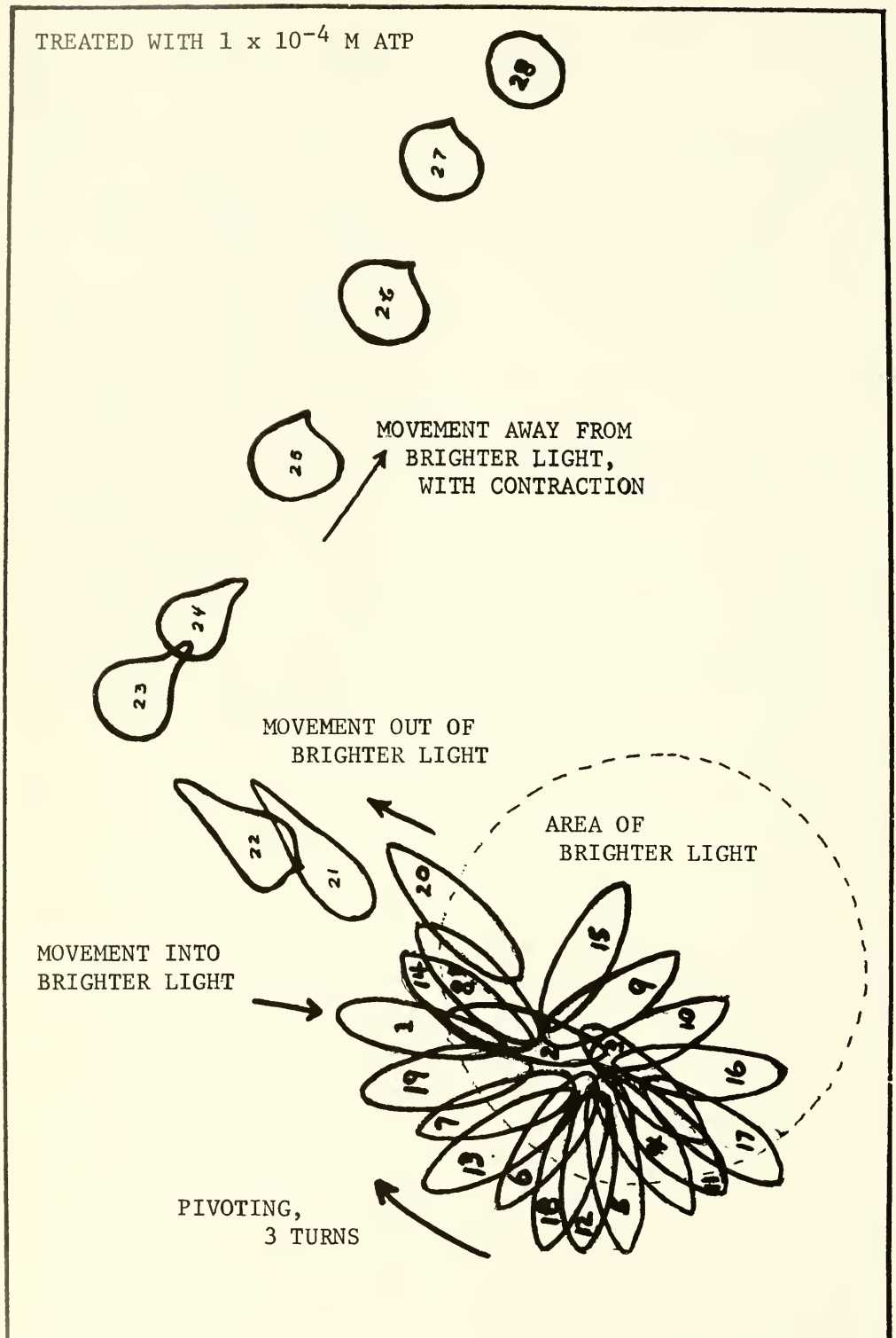

FIG. 6. Path of *Euglena gracilis*, treated with 1 × 10^{-4} M ATP, on entering and leaving a spot of brighter light. A rapid pivoting occurs on entry and a rapid contraction of the cell on leaving the brighter spot. Traced from a motion picture sequence photographed at 200 frames per second, each picture in a sequence of 28 frames traced to show the reactions.

DISCUSSION

The above results indicate that not only is ATP the energy-source for flagellar movements, but that it is involved also in the photophobic response. The flagellum is the only organelle *Euglena* has which enables it to swim and perform the phototactic movements which occur when it alters direction of swimming (Jahn & Bovee, 1968). Hence, any circumstances which alter the availability of energy as ATP should and do alter both flagellar motility and beat frequency (Danforth, 1953; Brokaw, 1965; Diehn & Tollin, 1967) and therefore should and do alter phototactic movements (Diehn & Tollin, 1967). The swimming rate of *Euglena gracilis* is greatest at 40 ft. candles, which is the saturating level for the photophosphorylating mechanisms which produce ATP, and both ATP levels and swimming rates rise as the luminar intensity increases toward 40 ft. candles (Wolken, 1967). The helical undulations along the flagellum are intermittent ("interrupted helical waves"; Jahn & Bovee, 1968), probably dependent for origin on periodically initiated waves of chemomechanical interactions (PM pulses; Thornburg, 1967) requiring ATP energy.

Our results show that the energy from the extraneous ATP is taken up rapidly from solution and is used immediately and directly by the flagellum. ATP is a relatively large molecule. It may or may not be taken up as an intact molecule. It appears perhaps likely that transphosphorolase enzymes at the membrane of the flagellum may detach the ~Ph and transfer it to nucleotides within the flagellar matrix adjacent to inner side of the membrane and associated with the fibrils of the axial cylinder. This assumption is similar to that of Siekevitz & Potter (1965) for ~Ph transfer from mitochondria to cytoplasm without loss of mitochondrial nucleotides. Such a system of uptake would explain the speed and intensity with which *Euglena* responds to the presence of ATP in the surrounding medium.

The presence of an actomyosinoid chemomechanical motile machinery as the basis for all kinds of protoplasmic movements, including those of cilia and flagella, is well supported by a variety of evidence (see reviews by Kamiya, 1959; Gibbons, 1968; Brokaw, 1966; Holwill, 1966; Jahn & Bovee, 1967, 1968, 1969; and others). The flagellum of *Euglena,* like an actomyosin system, requires ATP as an energy source and both Mg and Ca ions are needed to maintain motility (Wolken, 1967). The detached, glycerinated flagellum of *Euglena* swims freely in critical amounts of ATP and those ions (Mahenda, et al., 1967).

The facts that available ATP up to a critical level accelerates the flagellar movements of *Euglena* and increases of ATP above that inhibit and stop flagellar movements resemble similar effects of ATP on other actomyosinoid systems of cells (Hoffman-Berling, 1960) and on muscle-actomyosin extracts (Weber, 1959).

If the mechanochemical pulse which initiates flagellar undulations is dependent on critical cations and especially on ATP levels both in the cell and along the flagellum, as appears probable, then variation of ATP concentration should produce all the effects we have noted on swimming rate and photophobic response.

Gössel (1957) showed that the paraflagellar photoreceptor swelling of *Euglena* conveys the energy of sudden increases of luminar-intensity to the flagellum, altering its position and increasing the amplitude of its undulations, producing the photophobic response. Diehn (1969b) found the normal energy quantum producing the photophobic response to be above an equilibrium of 2×10^{-5} ergs/cm^2 sec. Our results show that available ATP at certain concentrations augments

photophobic movements, the duration of capability for such responses, and apparently lowers the threshold for the shock reaction to the level of the photophobic response.

Since the movements of the flagellum depend on critical concentrations of cations as well as ATP levels (Wolken, 1967), ion fluxes, especially of Ca^{2+}, Mg^{2+}, K^{+}, and H_3O^{+}, are required concomitantly and in advance of the ATP-utilization sequence which produces the undulatory movements of the flagellum.

How the photoreceptor stores energy and releases it to the flagellum upon changes of luminar intensity is not known. Enzymes and photosensitive pigments in it have been suggested, but not yet found (Pringsheim, 1956; Wolken, 1969). Recent indirect evidence using potassium iodide (KI) as a specific inhibitor suggests that certain flavins are involved and may be resident, perhaps as crystals resembling amino-acid oxidase, in the paraflagellar photoreceptor (Diehn and Kint, 1970; Tollin & Robinson, 1969).

A recent theory by Bovee and Jahn (1972) suggests that since the photoreceptor of *Euglena* is crystalloid (electron-micrographs, Arnot & Walne, 1967; Leedale, 1967; polarized-light sensitivity, Diehn, 1969b) it may be piezoelectric, i.e., generates a current when deformed, or is deformed as it generates a current. Its poised crystalloid flavin molecules, assuming it has them, may absorb light-energy, generate a current and discharge a poised oxidation-reduction system (Jahn, 1963). Diehn (1970) suggests that as little as 4 photons of difference in luminary intensity above or below the poised level may be enough to excite phototactic movements and reorientation of the flagellum and body. Therefore, the photoreceptor may be able to deliver discharge of current into the flagellum during deformation of its crystalloid structure as light strikes it, i.e., it is a photoelectric body. The same theory, extended (Bovee & Jahn, 1972), assumes that flagellar fibrils are also quasi-crystalloid and are either piezoelectric or semiamorphous conductors, along which piezoelectric currents (resulting from bending the fibrils) translocate cations to and from cardinal sites (Ling, 1962) where they are able to set up the ionic state required for ATP-splitting. These flagellar pulses (PM pulses, Thornburg, 1967) originating at the flagellar kinetosome as a mitochondrial-ATP-powered red-ox discharge, precede as an electronic and cationic wave the motile ATP-splitting undulation. Any energy released from the photoreceptor during reaction to increased luminar intensity would augment the ion fluxes, the ATP-splitting and the flagellar movements (Bovee & Jahn, loc. cit.).

The availability of extra ATP-energy to load the energy reservoir to a "hair trigger" level in setting off the red-ox discharges at the flagellar kinetosome should increase the potential number of red-ox discharges/sec, and therefore the number of undulations/sec. The increased ATP-availability and utilization in the flagellum should augment the rate at which the undulations proceed along the flagellum, and depending on cation-associations, and dissociations, including H-bonds, the amplitude of the wave. The increased number and speed of undulations along the flagellum increases the thrust of the flagellum, and therefore the swimming rate/sec.

In summary, our results support the contentions of Wolken (1967) that swimming rate is linked to available ATP levels and of Bound and Tollin (1967) that both motility and phototaxis are related to available ATP levels.

There are two separate responses to light indicated: (1) A "light-on" response which is elicited as a photophobic response

with violent whirling of the flagellum, occurring if light intensity is increased suddenly and sufficiently; (2) A "light-off" response, elicited as the *Euglena* leaves an area of increased light intensity that is too weak to elicit a photophobic response, resulting in a change of direction; or, on leaving a field of intensity sufficient to have caused the photophobic response, or with added ATP, causing contraction and temporary cessation of movement.

These separate responses tend to support Diehn's contention (Diehn, 1972) that *Euglena* may have two photoreceptor mechanisms, one for light of lower intensities and another for light of higher intensities.

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THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

ALLEVIATION OF THE TOXICITY OF COPPER TO *TETRAHYMENA PYRIFORMIS* BY NONTOXIC IRON

By

Eugene C. Bovee, David A. Kegley, David Sternshein,
Ellen Wyttenbach and Barton L. Bergquist

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Alleviation of the Toxicity of Copper to *Tetrahymena pyriformis* by Nontoxic Iron.[1]

* Eugene C. Bovee, David A. Kegley, David Sternshein, Ellen Wyttenbach and Barton L. Bergquist[2]

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ABSTRACT

Copper (as $CuCl_2$) is toxic to and retards growth of *Tetrahymena pyriformis* at 3 to 5 parts per million in a proteose-peptone growth medium. Iron (as $FeCl_2 \cdot 4H_2O$) is stimulatory to growth in 3 to 15 ppm. Equal amounts of iron and copper together stimulate growth, most so at 15 ppm Cu with 15 ppm Fe. Unequal amounts of them are also stimulatory, the most so being 15 ppm Cu with 10 ppm Fe. Copper apparently inhibits mitochondrial synthesis of adenosine triphosphate, acting on flavinoid pigments and cytochromes by preempting sites normally occupied thereon by iron. Iron, in turn, lifts the block by displacing the copper at those sites. Stimulation of growth by the combined copper and iron may be due to the role of copper in the enzyme systems that form the iron porphyrins of the cytochrome system and its presence in polyphenol oxidases and tyrosinase.

INTRODUCTION

Toxicity of heavier metals to animals, protozoan to human, is well-documented (reviews: Bremer, 1974; Hartung, 1972; Louria, 1972). Most heavy metals are toxic, often lethal, to animals in amounts of 20 parts per million or less in water. The presence of toxic heavy metals in water-sources causes concern, both because of their immediate danger to the survival of certain small organisms involved in biodegradation and the danger to larger animals, including man, that may be poisoned by the metals as they are concentrated by progression through the food-webs of nature.

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Copper is toxic to humans (Louria, loc. cit.), livestock (Bremer, loc. cit.), poultry and game birds (Henderson, 1975), fish (Christensen et al., 1972; Stephenson and Taylor, 1975), annelids (Hartung, 1972), crustacea (Chaisemartin, 1973), insects and their larvae (Hartung, 1972) and protozoa (Cairns and Dickson, 1970; Roth et al., 1968), and to phytoplankton (Rice, 1973). The well-known toxicity of copper and other heavy metals to many fungi and bacteria is cited in most general textbooks of microbiology (e.g., Salle, 1948).

Nonetheless, copper is sometimes a necessary trace element, required for blood-pigments of certain invertebrates (Elvehejm, 1935), some enzyme systems of vertebrates (Schulze, 1941) and invertebrates, e.g., *Tetrahymena pyriformis* (Hill, 1972). It is also involved in the production of iron-porphyrins in vertebrate animals (Schulze, 1941).

While much effort has been directed toward determining toxicity of heavier metals, little has been done to determine if nontoxic chemicals normally present in aquatic organisms and their environments may alleviate or block the toxicity of the heavier metals. Some studies show that small amounts of one toxic metal may alleviate the effects of another one, e.g., the well-known copper-molybdenum antagonism (e.g., Suttle, 1974). A few studies show that organic chelaters may reduce ions of heavier metals from water to nontoxic levels, e.g., chelation of copper by ethylene-diamine-tetracetate (EDTA) (Stephenson and Taylor, 1975). The subject of naturally occurring ions as counters to toxicity appears to be relatively uninvestigated, although it is generally conceded that "hard" waters can carry a greater burden of toxic metals than "soft" waters.

We have tested the effects of iron (Fe^{++}) as a counter-ion against the toxicity of copper (Cu^{++}) for the growth of the ciliated protozoon, *Tetrahymena pyriformis*, to determine to what degree the iron alleviates the toxicity of the copper.

MATERIALS AND METHODS

Tetrahymena pyriformis (Clonally derived from Strain HSM) were grown axenically and synchronously dividing (Scherbaum and Zeuthen, 1955) at 29°C $\pm$ 0.2° in 250 ml of proteose-peptone medium (Elliott and Hayes, 1955), lacking the yeast-extract fraction, in 500 ml screw-capped, sidearm Ehrlenmeyer flasks at 29°C $\pm$ 0.2 degree. About 30,000 *Tetrahymena* were used as each inoculum for control and experimental cultures. Counts of cultures were made by hemocytometer and Whipple cell methods to determine at what spectrophometric, light-transmittance reading a midway-logarithmic growth of 200,000 organisms/ml is indicated.

For experiments, *Tetrahymena* were grown in media containing: (A) Cu^{++} at 3, 5, 10 or 15 ppm; (B) 3, 5, 10, or 15 ppm Cu^{++} with, also, equivalent Fe^{++} (i.e., 3 ppm Cu^{++} plus 3 ppm Fe^{++}, etc.); (C) Cu^{++} 15 ppm plus 5 ppm Fe^{++}; (D) Cu^{++} 15 ppm plus 10 ppm Fe^{++}. Solutions were made with Cu^{++} as $CuCl_2$ and Fe^{++} as $FeCl_2 \cdot 4H_2O$, since Cl^- in the dilutions used is non-noxic to *Tetrahymena*.

All experiments were run three times, in triplicate each time, and mean growth curves plotted. Light transmittance was measured twice per day, in most experiments, after inoculation of cultures (or once per day in some experiments) for 5-7 days, until peak growth had been reached and decline of the population began.

RESULTS

1. CONTROLS—Rates of growth began with a brief lag phase of 15 to 20 hours, then entered the logarithmic phase

of growth which continued through the next 24 to 30 hours. Control populations continued to increase non-logarithmically through another 20 to 40 hours to asymptote before beginning to decline (Fig. 1). Populations reached about 450,000 to 500,000 per ml before decline began.

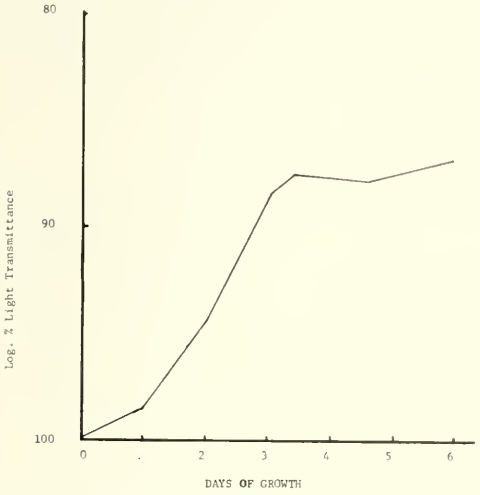

FIG. 1. Growth of *Tetrahymena pyriformis* in proteose-peptone medium at 29° C.

2. EFFECTS OF COPPER—Copper, alone, retarded the growth of *Tetrahymena* in as little as 3 ppm, growth always being slower and peak populations less numerous than the controls. The lag phase of the growth was lengthened, the logarithmic phase shortened and/or depressed and the asymptote was reached at a lower population density than for controls. Growth decreased as the concentration of Cu^{++} was increased with 20 ppm Cu^{++} almost completely eliminating growth (Fig. 2).

3. EFFECTS OF IRON—In concentrations of 3 to 15 ppm, Fe^{++} was stimulatory to growth, most significantly at 5 ppm, less so at 3, 10 or 15 ppm (Fig. 3).

4. EFFECTS OF EQUAL AMOUNTS OF IRON AND COPPER TOGETHER—At equal concentrations of both Cu^{++} and Fe^{++}, the latter eliminated

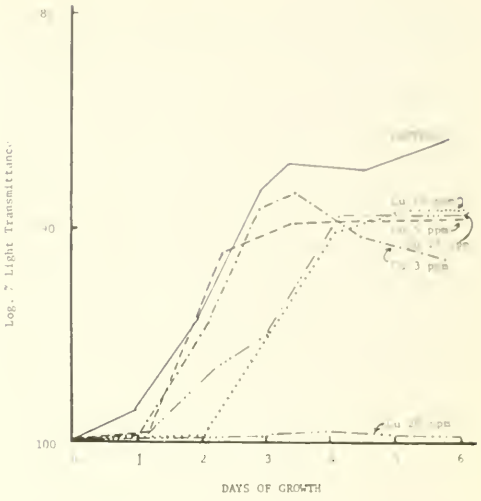

FIG. 2. Growth of *Tetrahymena pyriformis* with 3 to 20 parts per million of copper as $CuCl_2$.

the toxic effects of the former. At 3 ppm of each, growth exceeded both that with Cu^{++} alone (3 ppm) or of the controls grown at the same time, but not that with Fe^{++} alone at 3 ppm. At 5 ppm each of Cu^{++} and Fe^{++}, growth exceeded that with Cu^{++} at 5 ppm, or of the controls, and parallelled and ultimately exceeded the stimulated growth with Fe^{++} alone at 5 ppm. At 10 ppm each of the Cu^{++} and Fe^{++}, growth significantly exceeded both

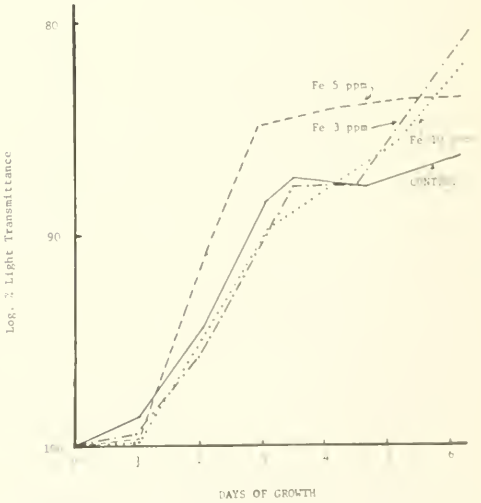

FIG. 3. Growth of *Tetrahymena pyriformis* with 3 to 10 ppm of iron as $FeCl_2 \cdot 4H_2O$.

growth with 10 ppm Cu^{++} alone, or the controls, and also exceeded growth with 10 ppm Fe^{++} alone. At 15 ppm each of Cu^{++} and Fe^{++}, growth significantly exceeded the growth with 10 ppm Cu^{++} alone, or 10 ppm Fe^{++} alone, or the controls (Figs. 4-7).

5. EFFECTS OF UNEQUAL AMOUNTS OF Cu^{++} AND Fe^{++}—At 15 ppm Cu^{++} and 5 ppm Fe^{++}, the latter only temporarily alleviated the toxic effects of the former, growth being initially faster, but not reaching as high a peak, and declining more quickly than with 15 ppm Cu^{++} alone. At 15 ppm Cu^{++} and 10 ppm Fe^{++}, growth ultimately and significantly exceeded that in other combinations tested, except for early growth where it was temporarily slower than the controls, or that with 15 ppm Fe^{++}, alone, or that with 15 ppm Cu^{++} plus 15 ppm Fe^{++}. The growth in the latter exceeded growth of all other combinations in early stages and was exceeded in later stages only by the growth with 15 ppm Cu^{++} plus 10 ppm Fe^{++} (Figs. 8, 9).

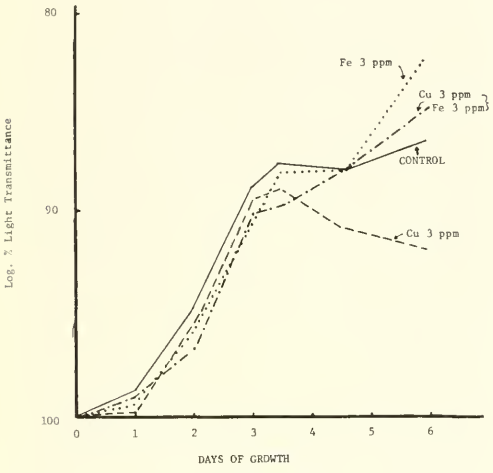

FIG. 4. Growth of *Tetrahymena pyriformis* with copper and iron in equal amounts of 3 ppm.

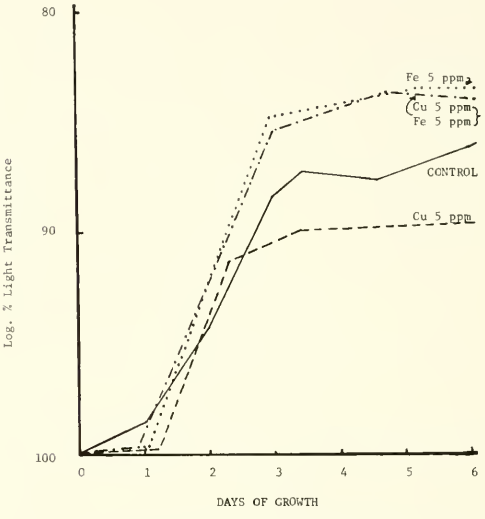

FIG. 5. Growth of *Tetrahymena pyriformis* with copper and iron in equal amounts of 5 ppm.

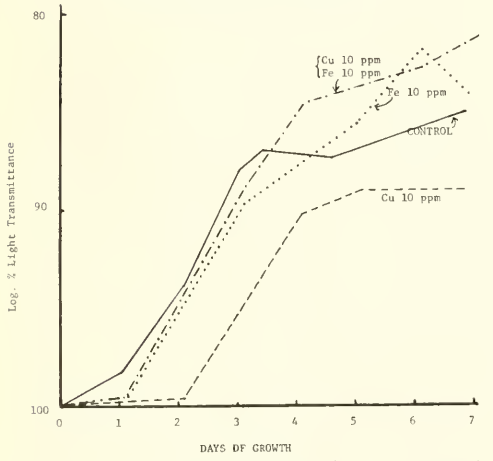

FIG. 6. Growth of *Tetrahymena pyriformis* with copper and iron in equal amounts of 10 ppm compared to growth with 10 ppm of copper alone, to growth with 10 ppm of iron alone, and to the control rate.

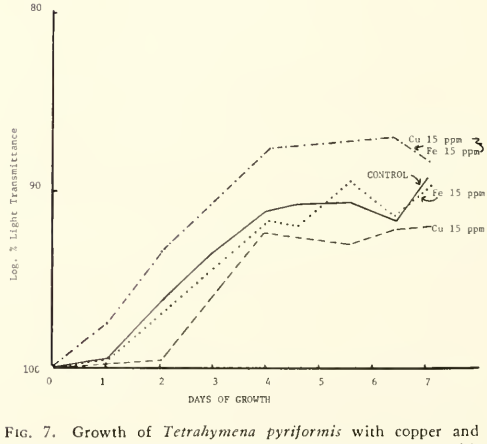

FIG. 7. Growth of *Tetrahymena pyriformis* with copper and iron in equal amounts at 15 ppm compared to growth with 15 ppm of copper alone, to growth with 15 ppm of iron alone and to the control rate.

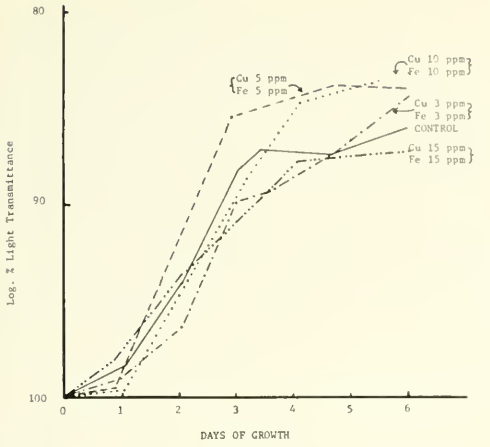

FIG. 8. Growth of *Tetrahymena pyriformis* with copper and iron together in equal amounts at various concentrations.

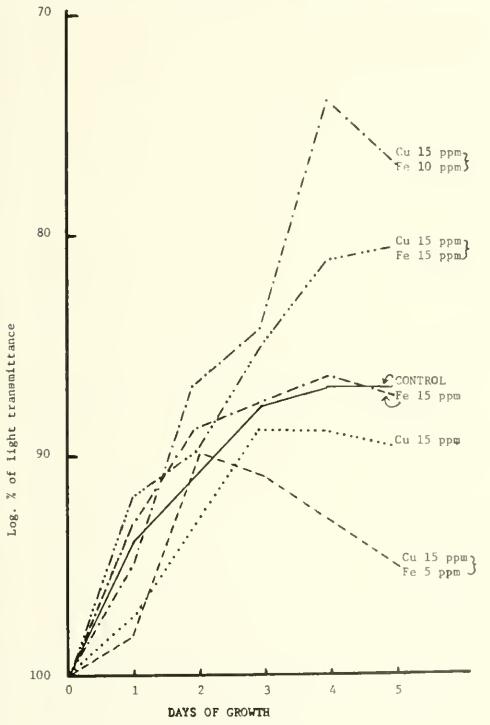

FIG. 9. Growth of *Tetrahymena pyriformis* with copper and iron together in unequal amounts at various concentrations.

DISCUSSION

Iron obliterates the toxicity of copper at concentrations of the latter which are detrimental to growth and survival of small aquatic organisms, such as *Tetrahymena pyriformis*. Some data indicates that other biologically non-toxic metals may reduce the toxicity of heavy metals, e.g., calcium vs. cadmium (Bergquist, 1974) or potassium, sodium or magnesium vs. cadmium (Bovee, unpublished).

Iron, calcium, potassium and magnesium, as ions, are critical triggers for major, cellular, enzyme-systems, e.g., those involved in making and using adenosinetriphosphate (ATP). Evidence from electronmicroscopy and biochemistry indicates that toxic, heavy metals poison these enzyme-systems, especially at cellular and mitochondrial membranes (Organ, 1972; Bergquist, 1974) by displacing requisite ions, thereby inhibiting energy-utilization and storage.

Added Fe^{++} evidently prevents the attachment of Cu^{++} to the sites where iron is required, particularly at the cytochromes and flavinoid electron acceptors.

Why the combination of copper and iron is stimulatory (except where copper is relatively high and iron much lower in concentration) we have not determined. Iron alone is stimulatory to growth of *Tetrahymena pyriformis* (Shug et al., 1969) and traces of copper are necessary for growth of *Tetrahymena* (Kidder and Dewey, 1951) and other organisms, invertebrate (Elvehejm, 1935) or vertebrate (Heilbrunn, 1952).

For vertebrates, copper and iron are both involved in the formation of hemoglobin and the concomitant release of iron from the liver (Schulze, 1941). For certain invertebrates, e.g., crustacea, copper is a component of the blood pigment, hemocyanin. It is also present in certain polyphenal oxidases and tyrosinase (West and Todd, 1957).

Despite a minimal requirement for copper by many animals, excesses are toxic, blocking enzymes critical in the tricarboxylic acid cycle, e.g., succinic dehydrogenase (Heilbrunn, 1952), and ribonucleases (Roth, 1959). Copper is also highly toxic for other small invertebrates in undetermined manners, e.g., heliozoa (Roth, et al., 1968).

Neither the toxic effect of the copper, nor its minimal requirement are fully explained. We assume that excesses of it, in addition to poisoning sites in enzymes normally occupied by iron, also block the succinic dehydrogenase of the tricarboxylic acid cycle, thereby doubly blocking that cycle, both at its "bridge" from glycolysis and by way of the flavinoid-cytochrome chain, where the copper displaces iron.

The iron can presumably displace or prevent attachment of the copper at sites where iron normally occurs, protecting those sites. The copper then, presumably, acts normally at and is readily available only to sites on enzyme systems where it is required, resulting in the combined stimulatory effect to growth, since both more iron and more copper are available to enzymes systems which require them.

In the environment, excesses of copper are less likely to be toxic where iron is also present, if the data found here may apply to other small, aquatic invertebrates and vertebrates as well as to *Tetrahymena*. Since the general, nutritional requirements of *Tetrahymena* are similar to those of many other animals (Hill, 1974), the extrapolation is reasonable.

This would further suggest that industrial effluents containing copper could more safely be introduced into waters with a relatively high content of iron than into waters lacking iron.

Industries unavoidably releasing some copper into local waters might better be located, therefore, in areas where waters naturally contain iron than in areas where iron content of the water is minimal to absent.

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POPULATION DYNAMICS AND PRODUCTION OF *DAPHNIA AMBIGUA* IN A FISH POND, KANSAS

By

Chi-Hsiang Lei
and
Kenneth B. Armitage

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ABSTRACT

High population and egg density of *Daphnia ambigua* Scourfield occurred in winter and spring when temperatures were low and food concentrations were high. Mean clutch size ranged from 1 to 5.7 with an average of 2.01 ± 1.12 (S.D., $N = 86$) while the number of eggs per adult female ranged from 0 to 5.1 with an average of 1.09 ± 0.98 (S.D., $N = 91$). Highest values usually occurred during population increase and high food concentrations. There was no consistent relationship between clutch size and size of the reproductive females. When mean clutch size was low, clutch size did not increase with increasing size of females carrying the eggs. The size of reproductive (parthenogenetic) females was generally larger during the winter and early spring

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when water temperatures were low and food concentrations were high. Population density, egg density, clutch size, and egg number per adult female were all positively correlated with the estimates of food concentration (seston and chlorophyll *a*) but were negatively related to temperature.

Sexual reproduction occurred in late March and April and lasted for about one month. Ephippial females did not appear when mean clutch size of parthenogenetic females was 1.0. Ephippial females appeared nearly two months later than males did. Instantaneous birth rate (b') fluctuated between 0 and 0.501 with an average of 0.067 for the period June 1972 to June 1973. Instantaneous birth rates were positively correlated with temperature but not the estimates of food concentration. The highest calculated instantaneous rate of population change (r') was 1.943 and the highest instantaneous rate of death rate was 1.589. Standing crop biomass ranged from 0 to 1.6 g dry wt/m^3 (0 to 8.4 kcal/m^3) with a mean of 251.1 mg dry wt/m^3 (1.3 kcal/m^3) for the period June 1972 to June 1973.

Production (somatic growth, P_g, and egg production, P_r) was estimated by egg ratio method and Winberg's method. Estimates of daily and monthly production calculated by the two methods were different but the estimates for the entire study period were similar, 6.8 g dry wt/m^3 (34.7 kcal/m^3) and 6.6 g dry wt/m^3 (33.1 kcal/m^3), respectively. The total production of resting eggs, 66.4 mg dry wt/m^3 (390.8 cal/m^3) was about 1% of the total production ($P_g + P_r$ + resting eggs) for the entire study period. The P/B coefficients estimated from dry weight and from caloric content were similar. The monthly P/B ratios ranged from 1.1 to 7.7 and were generally higher in the warmer months than in colder months. The annual P/B ratio was 25. The average daily P/B for the period June 1972 to June 1973 was 0.068 and that for the period July 1972 to June 1973 was 0.066. Therefore, the average biomass turnover time was 14.7 and 15.2 days, respectively. Daily P/B ratio was related more closely to temperature than to food. The monthly production of exuvia (P_{ex}) varied from 18.3 to 2752.8 cal/m^3, and the total P_{ex} for the period July 1972 to June 1973 was 11.2 kcal/m^3. P_{ex} contributed 9% ~ 49% to monthly $P_g + P_r + P_{ex}$ and accounted for 25% of annual $P_g + P_r + P_{ex}$.

INTRODUCTION

Detailed biological and ecological studies of member species are essential for the understanding of the structure and dynamics of ecosystems. In order to compile an energy budget for a natural zooplankton population and to understand how populations respond to environmental changes, data on population dynamics and production of the species concerned are required. Production estimates can be used to assess the relative importance of various species in the economy of the zooplankton community (Petrovich *et al.*, 1961; Patalas, 1970; Comita, 1972; Schindler, 1972). Production estimates also yield turnover rate information which can be used to evaluate the effect of environmental factors on zooplankton and to compare aquatic systems (Stross *et al.*, 1961; Winberg *et al.*, 1965; Patalas, 1970; Pederson *et al.*, 1976).

Daphnia ambigua Scourfield is a common and widespread zooplankter in aquatic communities of Kansas (Prophet and Waite, 1974). Because *Daphnia* are utilized directly or indirectly as food by young and adult fish, this organism could have a large impact on aquatic productivity. Information on population dynamics and production of planktonic crustaceans in Kansas is still very limited although several ecological studies on planktonic crustaceans are available (e.g. Armitage, 1961; Armitage and Davis, 1967; Armitage and Smith, 1968; Prophet, 1957; Prather and Prophet, 1969; Angino *et al.*, 1973; Prophet and Waite, 1974; Palavanchuk, 1977). The purpose of the present study was to analyze the population dynamics and estimate the production of a wild population of *Daphnia ambigua* in a fish pond in Kansas with the hopes of stimulating further research in zooplankton production in this state.

DESCRIPTION OF THE POND

The pond chosen for the study is located on Campus West, University of Kansas, Lawrence. The pond when full had an area of about one hectare and a maximum depth of about five meters. Most of the drainage basin was covered by grasses and scattered deciduous trees. The pond was sometimes used as a source of water for other experimental ponds. Thus its water level, and consequently its

area and depth, varied as a function of precipitation, runoff, removal from near the bottom, and evaporation.

MATERIALS AND METHODS

Zooplankton Sampling and Analysis

Zooplankton were sampled at least twice weekly from June 1972 to October 1972 and less frequently (once every week or once every two weeks) from November 1972 to February 1973. From March 1973 to July 1973 zooplankton samples were collected once every second day. During the ice-free season, plankton samples were taken with a #10 silk bolting net fitted on a Clarke-Bumpus plankton sampler which was towed at a depth of 0.5 meter for a period of five minutes in the central, deeper portion of the pond. Samples were collected at night, usually 1 to 2 hours after sunset. One revolution of the Clarke-Bumpus sampler was assumed to equal four liters of water. When there was ice on the pond, a hole was cut through the ice at the center of the pond and a vertical column of water was taken during the day by lowering a Wisconsin plankton net with #20 mesh size to the bottom of the pond, leaving it there for 5 minutes, and then hauling it to the surface. All samples were fixed immediately with 95% ethyl alcohol and then preserved in a mixture of 95% ethyl alcohol and 2% formalin.

In the laboratory each sample was diluted with distilled water to a known volume (usually 100 to 200 ml) depending upon the number of plankters present in the sample. At least three one ml subsamples from each 100 or 200 ml of diluted sample were counted on a Sedgwich-Rafter cell under low power of a stereo-microscope. When the number of plankters in the sample was very low, the entire sample was counted.

To facilitate the analysis of the population composition of *Daphnia ambigua,* individuals in each sample were grouped into five categories similar to those of Lei and Clifford (1974): except females with carapace length equal to or larger than 0.721 mm without eggs or embryos in their brood chamber were considered adults.

The average number of individuals per ml of each species of Cladocera and Copepoda was calculated from the three one ml subsample counts. This average number was multiplied by 100 or 200, depending on the final volume of diluted sample, and then divided by the total number of liters of water from which the sample was obtained, to calculate the number of individuals per liter. For undiluted samples, the number of individuals in the whole sample was divided by the total number of liters of water from which the sample was obtained, to calculate the number of individuals per liter.

The carapace of animals belonging to category 1 was opened with fine needles, and the numbers of eggs or embryos in the brood chambers were counted under a dissecting microscope (32×). The term "egg number" is used irrespective of whether eggs or embryos were counted. The mean egg number per brood was calculated from a subsample of at least 25 females having eggs or embryos in the brood chambers.

To determine the egg density (No. of eggs or embryos per ml), all of the eggs or embryos in the 1 ml subsample were counted: these included eggs in brood chambers and those free from the brood chamber due to preservation.

Length measurements of 200 individuals (if available) from each sample were made from the top of the head to the base of the shell spine (total body length), and from the anterior margin of the carapace to the base of the shell spine (carapace length).

Physico-chemical Analysis

All water samples were taken with a 2.1-liter Kemmerer Water Sampler at 0.5 m intervals from the surface down to within 10 cm of the bottom of the pond, with the center of the water sampler at the depth being sampled. Samples were combined for the determination of plant pigments, dissolved solids, orthophosphate, nitrogen, and seston. All water samples were filtered through a #10 silk bolting net (mesh size 153 μm) to remove larger organisms and debris before any further analysis was performed.

The concentrations of orthophosphate, ammonium-N, nitrate-N, and nitrite-N were determined colorimetrically (Hach Chemical Company Manual 1969) with a Bausch and Lomb Spectronic 20 Spectrophotometer.

Alkalinity (Hach Catalog No. 9:5) and total dissolved solids (American Public Health Association, 1965) were determined using standard procedures. The pH of the pond water was measured with a IL 175 PORTO-matic pH meter; water temperatures were measured with a thermistor thermometer coupled to a galvanic cell oxygen analyzer (Precision Scientific Co., Chicago). Light penetration was estimated with a Secchi disc having a diameter of 20 cm.

Seston Analysis

The dry weight of the seston was determined from a 500 ml or 1000 ml sample, depending upon the concentration of seston. The sample was filtered through a dry, tared Whatman GF/C fiber-glass filter which had been pre-ignited at 500°C for 24 h. The filter with seston was dried at 60°C for 24 h and reweighed to determine the dry weight of seston; it was then ashed at 500°C in a muffle furnace for 30 minutes and reweighed to determine the ash content of the seston.

During the period between March 1973 and July 1973, the size distribution of seston particles was measured weekly by means of a Model Z_B Coulter-counter with a 140 μm-diameter aperture tube. Because pond water must be made saline to conduct electric current, an appropriate amount of sodium

chloride was added directly to the sample to get a salinity of 0.5% before counting (Mulligan and Kingsbury, 1968). When the concentration of seston was high (>36000 particles/ml), the sample was diluted with a 0.5% sodium chloride solution which had been filtered through a 0.45 μm Millipore membrane filter.

Plant Pigments

Phytoplankton for pigment analysis was concentrated from 500 to 1000 ml of sample (depending on the density of phytoplankton) onto a Whatman GF/C fiber-glass filter (5.5 cm diameter) placed in a Buchner type porcelain filter funnel fitted on a suction flask attached to a suction pump. The filter with phytoplankton was ground up in a porcelain mortar in 10 ml of 95% acetone. The whole was carefully pipetted into a 15 ml capped bottle which was wrapped with aluminum foil and placed in a refrigerator for 24 h. After 24 h extraction, the content of the bottles was centrifuged for 10 minutes and the optical densities of the supernatant were measured with a Zeiss PMQ II Spectrophotometer. The amount of chlorophyll *a, b, c* and carotenoid present in each sample was calculated (Strickland and Parsons, 1968).

Primary Productivity

Primary productivity was measured by the oxygen light and dark-bottle technique of Gaarder and Gran (1927). Dissolved oxygen was measured by azide modification of the Winkler technique (Amer. Public Health Assoc., 1965). In calculations, both PQ and RQ were assumed to be unity. The water samples were first strained through #10 silk bolting net to remove zooplankton and large debris.

Calorific Values

Seston

Dry weight of the seston was determined as described above except a 0.45 μm Millipore membrane instead of Whatman GF/C fiber-glass filter was used to concentrate seston. The filter with seston was carefully cut into small pieces, pressed into a pellet with a Parr pellet press, and burned in a Parr 1411 Semimicro Oxygen-bomb Calorimeter to determine the total calorific value of seston and filter. By subtracting the calorific value contributed by the filter, the calorific value of seston was thus obtained. The calorific value of 0.45 μm Millipore membrane filter was determined by burning a pellet of membrane filter. Four determinations of 0.45 μm membrane filter yielded a mean calorific value of 3053.7 ± 83.37 (standard deviation) cal/g with a coefficient of variation of 2.73%. This value is very close to the values obtained by Comita and Schindler (1963) and Moshiri (1968).

Daphnia ambigua

Calorific values were determined on *Daphnia* cultured in 15 gallon aquaria and fed abundantly with *Chlamydomonas*. Before collecting *Daphnia* from stock cultures for calorific determinations, they were starved for at least 12 days to avoid gut contamination and to produce egg-free females. The contents of the aquarium were first siphoned through a #00 silk bolting net (mesh size 0.752 mm) to separate adult females (total body length >0.87 mm, Group III animals), and were then strained through a #1 silk bolting net (0.417 mm mesh size) to separate medium size females (BL between 0.62 mm and 0.87 mm, Group II animals). Finally, the contents were strained through a #16 net to concentrate young females (BL < 0.62 mm, Group I). Size group I and II consisted of immature daphnids; size group III daphnids were all adults. Each group of daphnids collected on the net was flushed several times with distilled water and washed into a beaker. Animals in the beaker were further sorted with an eyedropper. After the complete separation, each group of animals was rinsed several times with distilled water and dried in an oven at 60°C for 24 h. The dry samples of each group of daphnids were then combined and mixed with an agate mortar, dried for another 24 h at 60°C, and stored in a crucible in a desiccator until the calorific determination was made.

Calorific value of *D. ambigua* was determined either by direct calorimetry or by the wet combustion method with potassium dichromate in concentrated sulfuric acid as oxidizing agent. In direct calorimetry, the sample (dry powder of *Daphnia*) ranging in weight from 4.5 to 10.5 mg was combined with 100 to 150 mg of benzoic acid and pressed into a pellet. Owing to the difficulty of obtaining a large sample of *Daphnia* for bombing, the use of benzoic acid as filler was necessary.

The wet combustion method was a modification of the procedure of Ostapenya (1965, described in Winberg, 1971). A dry, ground sample of *Daphnia* (weight 0.84 to 3.69 mg) was placed together with 100 mg of Ag_2SO_4 into a 125 ml combustion flask, and 10 ml of 0.1 N solution of potassium dichromate in concentrated sulfuric acid was then carefully added into the flask by allowing the solution to run slowly down the inner surface of the neck of the flask which was slowly rotated. The flask was swirled gently to disperse the sample in the dichromate-acid solution, and was then covered with a 50 ml beaker and heated for 60 min. at 140°C in a thermally regulated drying oven. After being heated, the flask was cooled to room temperature and the neck and wall of the flask were washed with 10 ml of distilled water. The 50 ml beaker, serving as a cover of the flask, was also washed with 5 ml of distilled water which was added to the flask. After adding 3 drops of phenyl-antranilic acid as an indicator, the excess dichromate remaining in the flask was titrated with a 0.02 N solution of ferrous ammonium sulfate ($Fe(NH_4)_2(SO_4)_2 \cdot 6H_2O$).

Two control blanks (each containing 100 mg of Ag_2SO_4 and 10 ml of 0.1 N dichromate-acid solution, excluding daphnid sample) were treated identically to the sample flasks and titrated with 0.02 N

ferrous ammonium sulfate solution. The amount of oxygen required to oxidize the sample was calculated from the amount of dichromate used and expressed as mg O_2/mg sample. This value was then multiplied by 3.4 (oxycalorific coefficient) to obtain the calorific value (cal/mg) of the sample.

In order to calculate the calorific value in terms of ash-free dry weight (cal/ash-free mg), the fraction of ash content in the sample was determined by two methods; direct combustion of samples of dry ground *Daphnia* in a muffle furnace at 500°C for 2 h (direct ignition method) and by further combustion for 2 h in a muffle furnace at 500°C after being burned in an oxygen bomb calorimeter for calorific determination (oxygen bomb method).

Eggs at stage I (Lei and Clifford, 1974) were dissected from adult females of laboratory cultured *Daphnia,* washed with distilled water, and dried for 24 h at 60°C. The dried eggs were stored in a crucible in a desiccator until the calorific determination was made by the wet combustion method.

Population Parameters and Production Estimate

Population Parameters

The instantaneous birth rate, b′ was calculated from the formula (Paloheimo, 1974)

$$b' = \ln\ (1 + E_o/N_o)/D \qquad (1)$$

Where E_o and N_o are the number of eggs or embryos (egg density) and the number of animals (population density), respectively; D is the embryonic (or egg) developmental time in days at the respective temperature. The egg developmental time (D in days) at the respective temperature (T in °C) was estimated from the equation, $\ln D = 3.48977 - 0.17960T + 0.00244T^2$ (Lei, 1979).

The finite birth rate (number of newborn per animal per day) was calculated from the formula (Caswell, 1972)

$$B = b'\ (e^{r'} - 1)/r' \qquad (2)$$

where b′ is instantaneous birth rate, and r′ is the instantaneous rate of population change. r′ was calculated from successive pairs of population counts from the formula (Hall, 1964)

$$r' = (\ln\ N_t - \ln\ N_o)/t \qquad (3)$$

Where N_o is the initial population size and N_t the population size after an interval of t days. This equation is based on the assumptions that eggs were produced and hatched continuously, and that the population age distribution approximated the stable form for the period between observations.

Knowing b′ and r′, the instantaneous death rate, d′, of the populations was calculated as:

$$d' = b' - r'$$

Production

Production is defined as the increase in biomass which occurs in a given period of time (or as the total quantity of biomass formed over a stated period), whether or not all of it survives to the end of that period (Mann, 1969).

Production estimates were calculated by dividing the standing crop biomass by turnover time. Turnover time was estimated from finite birth rate (Cummins *et al.*, 1969) as

$$T = 1/B$$

where T is the turnover time in days, and B, the finite birth rate. Thus production rate, P (mg/m³/day, or cal/m³/day) can be calculated as:

$$P = (\text{Standing crop biomass})/T$$

which is equivalent to

$$P = (\text{Standing crop biomass}) \cdot (B)$$

This method of production calculation will be referred to as "egg ratio method."

Length-frequency data and length-weight relationships (Lei, 1979) were used to convert standing crop numbers to standing crop biomass. They were calculated as:

$$\text{Biomass (mg dry weight/m}^3) = \Sigma N_j W_j + N_e W_e + N_{ep} W_{ep}$$

or

$$\text{Biomass (cal/m}^3) = \Sigma N_j W_j C_j + N_e W_e C_e + N_{ep} W_{ep} C_{ep}$$

where N_j is the number of individuals in different size groups; N_e, the parthenogenetic egg density; N_{ep}, the density of resting eggs; W_j, the dry body weight of different size groups; W_e and W_{ep} the dry weight of individual parthenogenetic and resting eggs, respectively; C_j the calorific value of *D. ambigua* (4.475 cal/mg dry weight for juveniles and 4.9236 cal/mg dry weight for adults); C_e the calorific value of parthenogenetic eggs (5.883 cal/mg dry weight) and C_{ep} the calorific value of resting eggs.

For comparison, production was also estimated from the formula of Winberg *et al.* (1965):

$$P\ (\text{mg dry weight/m}^3\text{/day}) = (N_e W_e)/T_e + (N_j \Delta W_j)/T_j + (N_a \Delta W_a)/T_a$$

and

$$P\ (\text{cal/m}^3) = (N_e W_e C_e)/T_e + (N_j \Delta W_j C_j)/T_j + (N_a \Delta W_a C_a)/T_a$$

where P is the production; N_e, N_j and N_a the number of eggs (or embryos), juveniles, and adults, respectively; W_e the weight of an egg; ΔW_j and ΔW_a the weight increment of juvenile and adult, respectively (i.e. the difference between the initial weight of given stage and the initial weight of the following stage); C_e, C_j, C_a the calorific value of eggs, juveniles, and adults, respectively; T_e, T_j, T_a the duration of development of eggs, juveniles and adults respectively.

The duration of juvenile (i.e. postembryonic developmental time, T_j in days) at the respective temperature (T in °C) was estimated from the equation, $\ln T_j = 4.00664 - 0.24266\ (\ln T)^2$ (Lei, 1979). T_a (average life span of adult) was calculated assuming the growth rate of body length in adults is approximately 3 times lower than in juveniles (Patalas, 1970; Weglenska, 1971), by

$$T_a = [3T_j(\bar{L}_a - L_{oa})]/(L_{oa} - L_{oj})$$

where L_{oj} is the initial body length of the juvenile (i.e. the body length of neonata), L_{oa} the body length of primiparia, and $\bar{L}_a$ the average body length of an adult individual in the investigated population. This second method of production estimation will be referred to as "Winberg's method."

The total production for the entire season was obtained by plotting daily production for the entire season and determining the area under the curve planimetrically.

Molting is a frequent occurrence in the life of crustaceans and each exuvium represents a significant fraction of dry weight of an individual. Wissing and Hasler (1968) reported a calorific value of 5.062 cal/mg dry weight (5.753 cal/mg ash-free dry weight) for the chitin of *Daphnia* which represented 15-20% of the calories of an individual. According to our calculation, based on a calorific value of 5.062 cal/mg dry weight for chitin and assuming that the chitin represents 15% of the calories of an individual *Daphnia,* the chitin represents on the average, 13.8% (13.0 to 14.5%) of the dry weight of an individual *D. ambigua.* Because growth of *Daphnia* is accomplished by regular molting, a significant amount of energy contained in the chitin is lost together with casted exuvia. Therefore, in the calculation of the energy budget for a considerable period of time, the amount of energy expended in exuvia must be considered.

To estimate the daily energy expenditure in exuvia by the *Daphnia* population, the amount of energy in the chitin was assumed to be 15% of the total calories of an individual *Daphnia,* and was calculated as:

$$\text{Molt (cal/m}^2\text{/day)} = (0.15N_jW_jC_j)/D_j + (0.15N_aW_aC_a)/D_a$$

when N_j and N_a are the density (No./m^3) of juvenile and adult *Daphnia;* W_j and W_a the mean dry weight of one individual of juvenile and adult *Daphnia;* D_j and D_a the duration of juvenile and adult instars (in days), temperature adjusted; C_j and C_a the calorific value (cal/mg dry weight) of juvenile and adult.

The duration of juvenile (D_j) and adult instar (D_a) at the respective temperature (T in °C) was estimated from the equation:

$$\ln D_j = 2.78332 - 0.15814T + 0.00214T^2 \text{ and}$$
$$\ln D_a = 3.41135 - 0.17707T + 0.00256T^2,$$

respectively (Lei, 1979). The total energy expenditure in exuvia for the entire season was obtained by plotting daily expenditure for the entire season and determining the area under the curve planimetrically.

RESULTS

Some Environmental Parameters

Detailed data of physico-chemical parameters are recorded in Lei (1979). Concentrations of orthophosphate were generally higher in 1972 than in 1973. Lowest values occurred in May and June 1973; highest values occurred in November 1972 and October 1973. The concentrations generally are in the high end of the range of concentrations typical of surface waters of lakes of humid-temperate regions (Hutchinson, 1957). The mean for the period of study was 0.045 mg/l ($\pm$ 0.060 SD).

Nitrogen occurred as ammonia, nitrate, and nitrite. Nitrite-N concentrations always were less than 0.01 mg/l. Nitrate-N concentrations varied from 0.007 mg/l to 0.141 mg/l with a mean of 0.0735 mg/l. Highest values occurred in early spring and in autumn; lowest values occurred in late spring and in the summer. The values of nitrate-N are higher than would be expected in natural waters, and may represent either an influx from run-off water from the pond basin or the nitrification of ammonia *in situ.* The concentration of ammonia-N exceeded the concentration of nitrate-N throughout the period of study. Lowest values occurred during the winter months. The concentrations and seasonal distribution of ammonia-N are not unusual for temperate freshwaters (Hutchinson, 1957).

Dissolved solids tended to be highest in the spring and lowest in the fall. The range of concentration was 145 to 309 mg/l with a mean of 202.3 mg/l.

Turbidity, by reducing light penetration, may affect the photosynthetic capacity of the primary producers. Secchi disc values were generally lower than would be expected for a typical North American lake. There was no clear seasonal pattern of transparency. The values varied between 16.8 cm and 260 cm with a mean of 157.89 cm.

Chlorophyll *a* is a measurement of the concentration of algae which could be food for *Daphnia.* Values ranged from 0.46 to 28.4 mg/m^3 (Fig. 1) with a mean

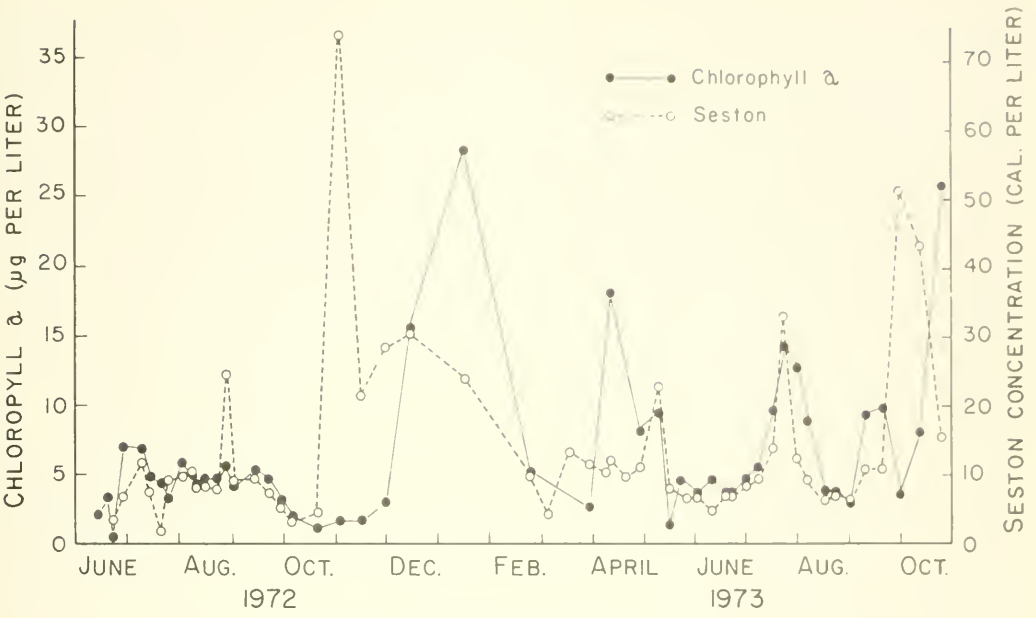

FIG. 1. Seasonal variation in chlorophyll *a* and seston in the Fish Laboratory Pond.

of 6.43 mg/m^3. The suspended matter, measured as seston, may also be a source of food. The range of seston concentrations, expressed as mg dry weight/l, was 1.1 to 73.5 mg/l with a mean of 10.3 mg/l. The highest concentrations of seston occurred in fall or winter. Most of the seston particles had a diameter between 2 and 8 µm. Particles of this size are readily selected as food by zooplankters (Edmondson, 1957; Brooks and Dodson, 1965; Gliwicz, 1969).

Temperature, pH, alkalinity and primary production were measured at more than one depth. However, for convenience, values of these parameters are reported as the average of all depths measured. Temperature varied from 4.2 to 29.9°C with a mean of 22.1°C. Temperature was relatively high by early June and peaked in late July and mid August. By late August water temperature began to decline but did not drop below 20°C until October (Fig. 2). Water temperature reached its minimum (4.2°C) by mid November 1972, and was maintained at near 5°C until February 1973. The water warmed rapidly in April, and reached 20°C in early June 1973.

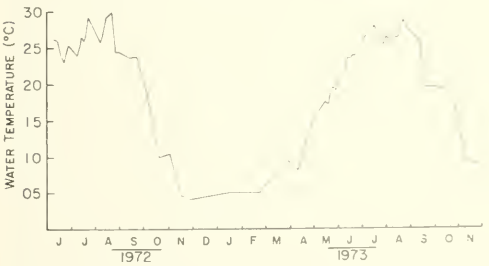

FIG. 2. Mean water temperature of the Fish Laboratory Pond.

pH varied from 6.7 to 9.5 with a mean of 8.3. The value gradually increased from near 8 in June to values higher than 9 in mid August through October. By early November pH dropped to less than 8 and pH remained between 7 and 8 (except for one value below 7) until June 1973 when the values again exceeded 8 (Lei, 1979).

The annual pattern of change of concentration of total alkalinity was similar to the pattern of pH. Values ranged from 52.8 to 147.7 ppm with a mean of 98.7 ppm

for the period studied. Total alkalinity exceeded 100 ppm through July 1972. Values decreased markedly in August and reached 50 ppm in September. Total alkalinity increased rapidly in November and remained above 100 ppm for the duration of the field work. Phenolphthalein alkalinity ranged from 0 to 17.2 ppm with a mean of 5.39 ppm for the period studied.

Rates of gross primary production were generally high throughout the summer of 1972. Rates during the winter were low, often one third or less the summer rates. Although rates increased in the spring of 1973, they remained much lower than they had been in 1972. The range of gross primary production of the period studied was 17.9 to 330.8 mg carbon/m^3/day with a mean of 146.3 mg carbon/m^3/day.

Calorific Value of Seston

The calorific value of seston collected from the Fish Laboratory Pond varied from 1320 to 3631 cal/g dry weight with a mean value of 2220.2 ± 648.0 cal/g dry wt (Lei, 1979). The calorific values of seston found in this study were lower than those reported for two Thames Valley reservoirs, England (Kibby, 1971), but similar to those reported for Coon Lake, Ontario, Canada (Schindler *et al.*, 1971).

The calorific value of dry matter in planktonic and benthic organisms is directly related to the ratio between the organic and mineral fraction in the dry matter of organisms (Ostapenya and Sergeev, 1963). The relationship between the calorific value and the percent of organic matter in aquatic organisms was described by either a linear (Sherstyuk, 1971, Thayer *et al.*, 1973) or a curvilinear (Platt *et al.*, 1969) regression equation. The relationship between the calorific value and the percent organic content of seston in this study was described by a linear regression equation as

$$Y = 224.4 + 43.9X$$

where Y is the calorific value of seston (cal/g dry wt) and X is the percent organic matter (i.e. 100 − %ash content). Both the correlation coefficient ($r = 0.9$, $df = 15$, $P < 0.001$) and regression coefficient ($b = 43.9$; $F = 107.0$; $df = 1,15$; $P < 0.001$) were highly significant.

Calorific Values of Daphnia and Eggs

The mean calorific value obtained by the wet combustion method for group I, group II, group III, and eggs was 3828, 4041, 4369, and 5188 cal/g dry weight, respectively (Table 1). They were all significantly different from one another ($P < 0.05$; Student-Newman-Keuls test, Sokal and Rohlf, 1969) indicating that the calorific content of *D. ambigua* changes with developmental stages. The change of calorific value with the developmental stages was reported for other animals by Richman (1958), Comita and Schindler (1963), Khmeleva (1968), Klekowski *et al.* (1967), and Kibby (1971). The mean calorific values obtained by direct calorimetry for group I, 4369 cal/g dry wt and for group III, 4924 cal/g dry wt were also significantly different from each other ($t = 3.02$, $df = 5$, $P < 0.05$).

The completeness of oxidation of organic matters by the wet combustion method (bichromate oxidation) was tested on several pure organic materials. The completeness of oxidation varied from 81.2% to 106.6% with a mean of 93.5 $\pm$ 5.9% (Lei, 1979). A comparison of the results obtained by the wet combustion method with those derived from direct calorimetry suggests that the completeness of oxidation of *D. ambigua* was 87.6% for group I and 88.7% for group III. The mean completeness of oxidation for these

two groups considered together, 88.2%, is close to the value of 90% obtained by Ostapenya (1965). Because calorific values obtained by the wet combustion method were lower than those obtained by direct calorimetry, the calorific values of group II and eggs obtained by wet combustion method were corrected for 11.8% (i.e. 100% − 88.2%) incomplete oxidation. The mean calorific values after correction were 4583 cal/g dry wt for group II and 5883 cal/g dry wt for eggs.

There was a significant difference between the values of ash content obtained by direct ashing of samples in a muffle furnace and by oxygen bomb combustion (Table 2). The t value for group I was 8.53 ($df = 4$; $P < 0.01$), and that for group III was 3.47 ($df = 7$; $P < 0.02$). The ash content determined from weight loss on ignition in oxygen bomb calorimetry was underestimated (Paine, 1964). Bomb combustion produced a systematic error of underestimate and a random error of variation between trials (Reiners and Reiners, 1972). These errors varied among the different types of material tested, but in general both types of error increased with the ash content of the material. The average systematic error of underestimate of ash content for all samples they tested was 1.46%, which led to an error of 1.56% when adjusting calorific coefficients to an ash-free basis. Oxygen bomb combustion produced an underestimate of ash content in the present study (Table 2). Therefore, the ash values obtained by direct ashing in muffle-furnace were used in calculating calories per gram ash-free dry weight for *D. ambigua*. The mean ash content of group I was significantly larger than the mean ash content of group II and group III. The ash content of group II and group III animals did not differ significantly. Because of the difficulty of obtaining enough sample for ashing, the ash content of the eggs of *D. ambigua* was not determined. If the ash value of 4.0% reported for the eggs of *D. galeata mendotae* (Moshiri and Cummins, 1969) is used, the cal/g ash-free dry wt of the eggs of *D. ambigua* would be 6128.

Seasonal Pattern of Zooplankton Abundance

Two species of Calanoida (*Diaptomus siciloides* and *D. clavipes*), three species of Cyclopoida (*Mesocyclops edax, Cyclops bicuspidatus thomasi, C. vernalis*) and one species of Harpacticoida (*Canthocamptus* sp.) occurred in the Fish Laboratory Pond. Detailed population data are recorded in Lei (1979).

Diaptomus (mostly *D. siciloides*) appeared throughout the study period; the population density (copepodids and adults combined) ranged from 1.2 (March 22, 1973) to 92.1 per liter (Aug. 7, 1972). The numbers were most abundant (above 22 individuals per liter) during the summer months of 1972 (June through mid September) and decreased in the following months and remained below 20/l through the fall and winter of 1972 and early spring 1973. The population increased to 65.4/l on April 24 of 1973 and then declined again. Population densities were comparatively lower in June and July of 1973 than in the same months of 1972.

Cyclops bicuspidatus thomasi was the most abundant cyclopoid. *Mesocyclops edax* and *C. vernalis* occurred sporadically. The population of all cyclopoids (copepodids and adults combined) was high during the summer months of 1972 and late spring and early summer of 1973. The highest density (60.4/l) occurred on May 18, 1973.

Nauplii of all copepods combined were most abundant during the early summer (late June and early July of 1972; late May and June of 1973). The numbers of

nauplii were low during the winter (1972) and early spring (1973). The highest density (50.8/l) appeared on June 8, 1973.

Fourteen species of Cladocera were identified in the pond with *Daphnia ambigua, Daphnia parvula* and *Ceriodaphnia lacustris* being the most abundant. *Diaphanosoma leuchtenbergianum* appeared in late June through mid October of 1972 with two population maxima, one on July 31 (6.2/l) and other on August 30 (8.3/l). *Diaphanosoma* was completely absent from the pond in the following months and had not appeared again by the end of July 1973.

Scapholebris kingi was present occasionally during June, July and October of 1972; density never exceeded 1.5/l. *Moina* sp. appeared in late June of 1972 but was not found in the early part of July 1972. It appeared again in late July and remained in the pond through August and early part of September 1972. The peak population (44/l) was found on August 22, 1972.

Chydorus sphaericus, the most abundant chydorid in the pond, was collected in most of the samples except those collected in late July and early August of 1972. The highest population density (43.5/l) occurred on November 1, 1972. Other chydorids (*Alona* sp., *Kurzia latissima, Leydigia quadrangularis* and *Pleuroxus* sp.) were collected occasionally in the samples and the numbers were insignificant.

Simocephalus sp. was present in spring of 1973, and early summer of 1972 and 1973, but the density was below 1.0/l.

Two species of *Ceriodaphnia* (*C. lacustris* and *C. reticulata*) were present in the pond, *C. lacustris* was predominant most of the time. The 1972 population of *Ceriodaphnia* had three peaks; the first on June 29 (227.1/l), the second on August 30 (145.7/l) and the last on September 21 (162.0/l). The population was completely absent from the plankton from November 26, 1972 until April 18, 1973. Brooks (1959) mentioned that the male of *C. lacustris* was not known from North America. However, some males of *C. lacustris* were found in the samples collected from the study pond. They appeared in late June, September, October and early November of 1972 along with ephippial females. Males and ephippial females also occurred in the population of *C. reticulata.*

Three species of *Daphnia* (*D. ambigua, D. parvula* and *D. pulex*) occurred in the pond. *D. ambigua* predominated during the colder season from November of 1972 through early June of 1973. *D. parvula* predominated in the warmer season from early July through early October of 1972 and completely replaced *D. ambigua* from mid-June through July of 1973. The highest numbers of *D. parvula* (173/l) were collected on August 22, 1972. *D. pulex* coexisted with each of the other species but the numbers generally were much lower because the size of *D. pulex* is about twice that of *D. ambigua* and *D. parvula,* the low numbers of *D. pulex* were probably the result of size-selective predation of fish (bass and bullheads) present in the pond (Hrbacek *et al.,* 1961; Brooks and Dodson, 1965; Galbraith, 1967; Brooks, 1968; Hall *et al.,* 1970; Nilsson and Pejler, 1973). The highest density (27/l) of *D. pulex* occurred on May 24, 1973. All three species of *Daphnia* produced males and ephippial females in this pond.

Six genera (*Asplanchna, Brachionus, Conochilus, Keratella, Lacane,* and *Platyias*) and one unidentifiable species of rotifers occurred in the study pond. Only populations of *Asplanchna* were enumerated. *Asplanchna* occurred from July 16 through October 3 of 1972, then completely disappeared until April 22, 1973. This species was most abundant in early and mid May of 1973. The highest population density (266.3/l) occurred on May 12, 1973. In 1973, a population pulse of an

unidentifiable species of rotifer occurred in March and a population pulse of *Conochilus*, lasted from May 26 through June 18.

Chaoborus larvae were also present in the plankton from June through October of 1972. They were most abundant from mid August through mid October of 1972 but were completely absent between early November of 1972 and mid May of 1973.

Population Data and Production Estimates

Standing Crop

The numbers of *D. ambigua* in the pond were very low from June through early August of 1972 (Fig. 3). The population

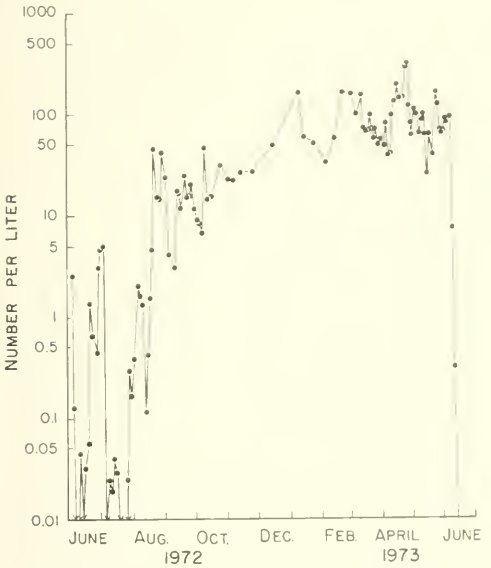

FIG. 3. Standing crop of *Daphnia ambigua* in the Fish Laboratory Pond. Arrows indicate when the population was zero.

disappeared on the 7th of June, reappeared on the 11th of June, and reached a density of 5.0/l on the 3rd of July. The population declined rapidly, disappeared again after the 16th of July and reappeared again on July 27, and numbers increased rapidly to 45.8/l by August 22. The numbers fluctuated considerably during September and October and then increased steadily to 168.4/l on January 10, 1973. Chlorophyll *a* concentrations also increased at this time (Fig. 1). The population declined in late January when the concentration of food decreased, then increased again to a high population level on February 22. A rapid decline in population density during late March and early April was associated with a bloom of an unidentifiable species of rotifer. Following the end of the rotifer bloom in late March, the numbers of *D. ambigua* increased rapidly at the same time food concentration increased and reached a maximum population of 319.6/l on April 26. A bloom of the colonial rotifer *Conochilus* in late May and early June, a low food concentration (Fig. 1), and rapidly rising temperatures (Fig. 2) were associated with the rapid decline of the *D. ambigua* population in early June. *D. ambigua* was not found after June 12 and was replaced by a population of *D. parvula*.

Population Composition and Size Distribution

The mean carapace length of females in the first adult instar, as determined from growth studies, was 0.721 mm (Lei, 1979). Although the smallest parthenogenetic female with eggs found in the field samples was 0.649 mm (Fig. 6), individuals equal to or larger than 0.721 mm without eggs or embryos were considered adults and those which were smaller were considered immature. On June 3 and June 5 no adults were ovigerous (Lei, 1979). The absence of recruitment was associated with the disappearance of *D. ambigua* after June 5. *Daphnia* present in mid June were all immature. These animals probably hatched from ephippia. This ex-ephippial population died out completely after July 16. After about 10 days a new population, consisting entirely of immature animals, probably hatched from ephippia. However, as the number

of reproductive females increased in the population, the population grew in the following months.

Males were present in late June and early July, and again on November 26 of 1972 but no ephippial females were found. All males present in this period were immature. In 1973, males first appeared on January 15, and were present until the population disappeared in June. The percentage of males present during the study period ranged from 0 to 29.6%. The highest percentage of males occurred on April 18 (Lei, 1979). Ephippial females first appeared on March 24 nearly two months later than males did. The highest percentage of ephippial females, 11%, appeared of April 22. The period of sexual reproduction lasted for about one month.

Females and males were grouped separately into 32 size groups (Lei, 1979). The size range of individuals and the maximum size an individual attained varied considerably throughout the study period. Generally, the largest size range and the largest animals were found at lower temperatures (December through early April, Fig. 6). When water temperature increased after early April, the maximum size of individuals tended to decrease.

Seasonal Variation in Egg Production and Body Size of Reproductive Females

All references to clutch size and number of eggs per adult female refer only to parthenogenetic eggs; ephippial eggs are excluded. Egg densities of *D. ambigua* during the summer and early fall of 1972 never exceeded 15.9/l. After mid October, egg densities increased rapidly to 471.1/l in January 1973 (Fig. 4). The increase of egg densities at this period was associated with a high mean clutch size (Fig. 5), a high standing crop (Fig. 3), and a large

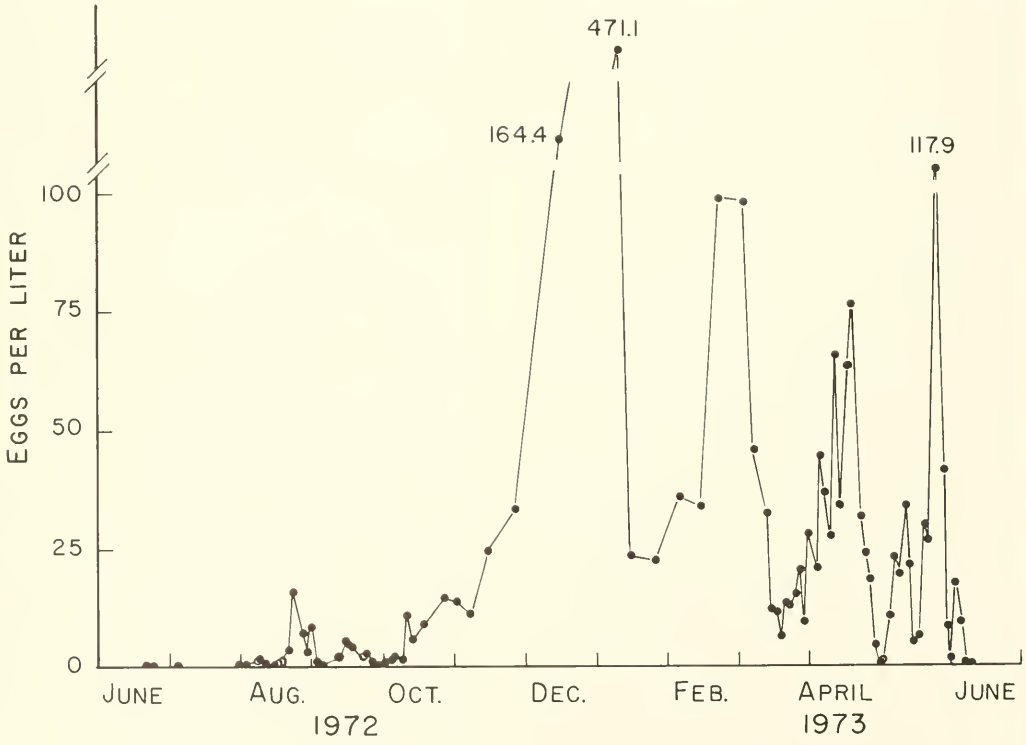

FIG. 4. Seasonal variation in the egg density of *Daphnia ambigua* in the Fish Laboratory Pond.

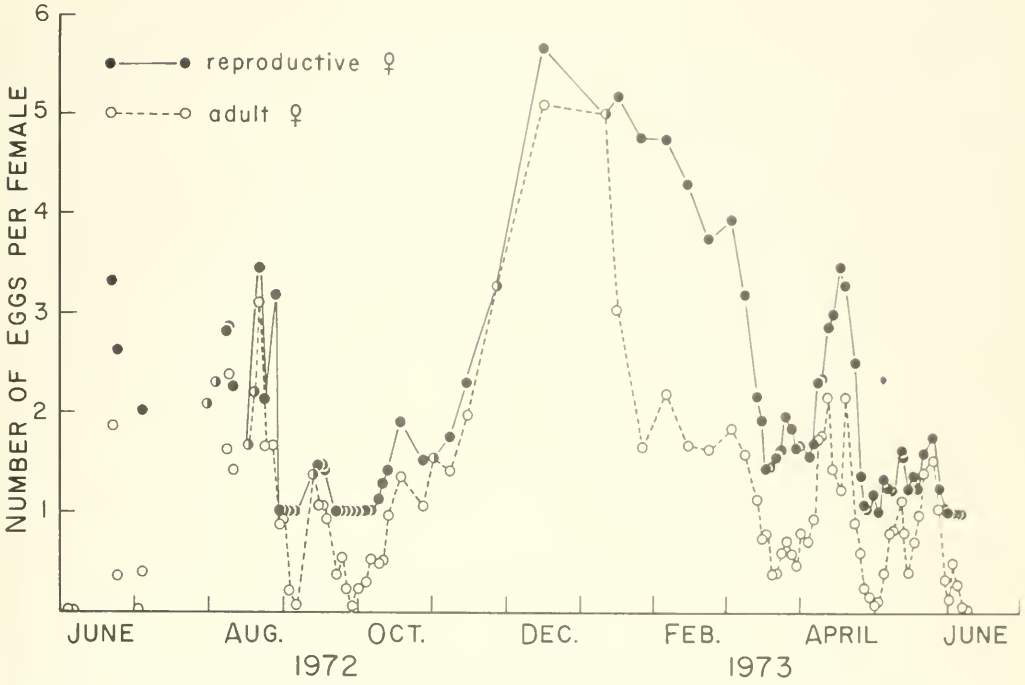

FIG. 5. Seasonal variation in the number of eggs per reproductive female and per adult female in the Fish Laboratory Pond.

proportion of reproductive females in the population (Lei, 1979). The subsequent decline in egg numbers was associated with a decrease in the number of reproductive females; mean clutch size remained high.

Egg numbers increased to a second peak in late February. A low, third peak of egg density occurred in mid April. This peak was associated with an increase in clutch size (Fig. 5); the number of reproductive females was low (Lei, 1979; Fig. 3). During late May, although mean clutch size was low, the combination of high population density and large proportion of reproductive females in the population produced a final peak of egg density (Fig. 4).

Mean clutch size ranged from 1 to 5.7 with an average of 2.01 ($\pm$ 1.12 S.D., $N = 86$), while the number of eggs per adult female ranged from 0 to 5.1 with an average of 1.09 ($\pm$ 0.98 S.D., $N = 91$). Highest values usually were associated with periods of population increase and high food concentrations (compare Figs. 1 & 5). The highest number of eggs per adult female and largest clutch size occurred in December 1972 and January 1973 (Fig. 5) when water temperature was low (Fig. 2) and food concentration was high (Fig. 1).

Ephippial females did not appear when mean clutch size of females was 1.0. During the month when ephippial females were present, the food concentration was higher than the period from May 31 to June 6 when mean clutch size was 1.0 and the number of eggs per adult female was low (Figs. 1 & 5). Because ephippial females of *D. ambigua* in the pond usually carried two resting eggs (occasionally three), food levels during the period when mean clutch size was 1.0 probably did not provide enough energy for the production of resting eggs.

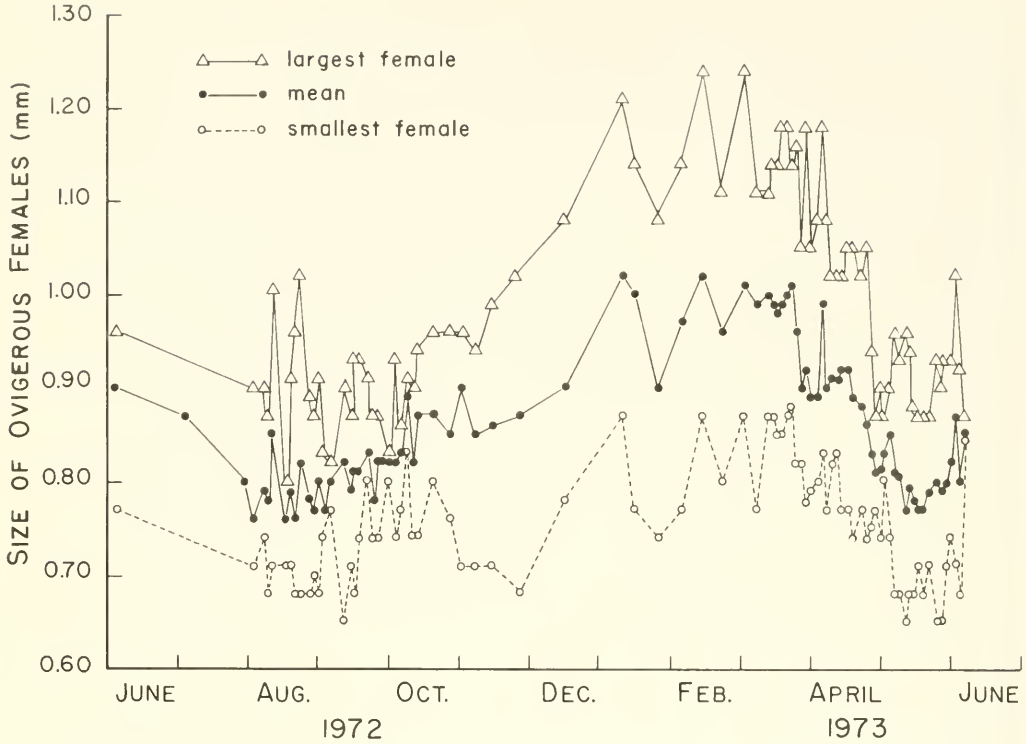

FIG. 6. Seasonal change in the carapace length of reproductive female *Daphnia ambigua* in the Fish Laboratory Pond.

Correlation coefficients were determined between body size and clutch size for 49 sampling dates; 34 values of r were significant ($P \leq .05$). All significant values of r were positive (Lei, 1979). When mean clutch size was low, clutch size did not increase with increasing size of females carrying the eggs. Furthermore, during early and late September of 1972 and early June of 1973, all size groups of reproductive females carried only one egg in the brood chamber (Fig. 5).

To test the relationship between food concentration and parthenogenetic egg production of *D. ambigua,* we calculated simple correlation coefficients between clutch size and available food and between egg number per adult female and available food. Index of available food was expressed as chlorophyll *a* (μg) or seston (cal) per liter at time t-n when the eggs were laid (where n is the time taken for eggs to develop at the respective temperature). Chlorophyll *a* or seston per liter was divided by the total number of *Daphnia, Ceriodaphnia,* and *Diaptomus* present per liter at time t-n to get chlorophyll *a* or seston per animal. For comparison, the index of available food was also expressed as chlorophyll *a* or seston per liter and simple correlation coefficients were calculated. There was significant, positive correlation between the parthenogenetic egg production of *D. ambigua* and the estimate of food concentration in the pond (Table 3).

Parthenogenetic egg production of *D. ambigua* was negatively correlated with temperature (Table 3).

The size of reproductive (parthenogenetic) females in the pond fluctuated considerably throughout the season, and was

generally larger during the winter and early spring when water temperatures were low and food concentrations were high (Figs. 1, 2, 6).

Population Parameters

Instantaneous birth rates (b′) fluctuated between 0 and 0.501 during the study period; highest values occurred in summer (Table 4). The instantaneous birth rate was significantly and positively correlated with temperature ($r = 0.38$; $df = 101$; $P < 0.001$) but was not correlated with estimates of food concentration ($r = 0.14$; $df = 101$; $P > 0.1$). Turnover time (of the number of individuals) ranged from 1.3 to 404.3 days.

The highest calculated rate of population increase (r′) was 1.943 and the highest rate of population decline was −1.589 for the period studied. Estimates of the instantaneous death rate (d′) were obtained by subtracting values of r′ from b′. Because the value of d′ depends on the difference between two quantities already calculated with error, it is the least reliable statistic associated with the egg ratio method (Edmondson, 1960). Thirty-nine negative death rates occurred among 100 estimates for the population of *D. ambigua*.

Biomass and Production

Population biomass ranged from 0 to 1.6 g dry wt/m^3 (0 to 8.4 kcal/m^3). Biomass was largest during winter and spring but was low in summer (Tables 4, 5). The mean biomass for the study period was 251.2 mg dry wt/m^3 (1.3 kcal/m^3) (Table 5).

Daily production was separated into growth and reproduction ($P_g + P_r$) and exuvia (P_{ex}). Daily $P_g + P_r$ estimates calculated by the egg ratio method (ERM) ranged from 0 to 157.5 mg dry wt/m^3 (0 to 783.8 cal/m^3), and those calculated by Winberg's method (WM) ranged from 0 to 129.3 mg dry wt/m^3 (0 to 673.3 cal/m^3) (Lei, 1979). The maximum daily $P_g + P_r$ calculated by each method occurred on May 24, 1973. When egg density and percentage of females carrying parthenogenetic eggs were high, the estimates of daily $P_g + P_r$ calculated by ERM were generally larger than those calculated by WM. When egg density and percentages of females carrying parthenogenetic eggs were low, the estimates derived from ERM were smaller.

Monthly $P_g + P_r$ estimated by ERM ranged from 1.3 mg dry wt/m^3 (6.5 cal/m^3) in June 1972 to 1.8 g dry wt/m^3 (9.6 kcal/m^3) in December 1972 while monthly $P_g + P_r$ estimated by WM ranged from 12.2 mg dry wt/m^3 (56.3 cal/m^3) in July 1972 to 1.5 g dry wt/m^3 (7.4 kcal/m^3) in May 1973 (Table 6). The monthly values calculated by ERM were smaller than those calculated by WM for most months but were larger during the colder months (November 1972 through February 1973) when egg production was high. Although monthly estimates of $P_g + P_r$ differed considerably, estimates for the entire study period were very similar, 6.8 g dry wt/m^3 (34.7 kcal/m^3) for ERM, and 6.6 g dry wt/m^3 (33.1 kcal/m^3) for WM (Table 6).

The $P_g + P_r$ estimates calculated by the two methods were averaged (Table 5). The daily production of resting eggs was calculated as $(N_{ep}W_{ep})/T_{ep}$ for mg dry wt/m^3/day and $(N_{ep}W_{ep}C_{ep})/T_{ep}$ for cal/m^3/day; where N_{ep} is the number of resting eggs per cubic meter, W_{ep} the mean dry weight of a resting egg and T_{ep} the time period required for the formation of an ephippium (equivalent to the duration of the adult instar). Because dry weight and calorific value of resting eggs were not determined, mean dry weight and calorific value of parthenogenetic eggs were used. The total production of resting eggs was obtained by plotting daily production for the period of

sexual reproduction and determining the area under the curve planimetrically. Sexual reproduction of *D. ambigua* occurred in March, April and May of 1973; the total production of resting eggs was 66.4 mg dry wt/m^3 (390.8 cal/m^3) which was about 1% of the total production for the entire study period (Table 5).

The P/B coefficients estimated from dry weight and from caloric content are similar (Table 5). The monthly P/B ratios ranged from 1.1 in February 1973 to 7.7 in August 1972, and were generally higher in the warmer months than in the colder months. The average daily P/B from June 1972 through June 1973 was 0.068 and from July 1972 through June 1973 was 0.066. Therefore, the average biomass turnover time was 14.7 and 15.2 days, respectively (Table 7).

Daily production of exuvia (P_{ex}) ranged from 0 to 233.8 cal/m^3 (Lei, 1979). Monthly P_{ex} varied from 18.3 cal/m^3 in July 1972 to 2.8 kcal/m^3 in May 1973, and the total P_{ex} from June 1972 to June 1973 and from July 1972 to June 1973 was 11.2 kcal/m^3 (Table 6). P_{ex} contributed from 9% in December 1972 to 49% in June 1973 to monthly $P_g + P_r + P_{ex}$, and accounted for 25% of annual P.

DISCUSSION

The ash content of *D. ambigua* was within the range of ash content reported by other workers (Table 8). The ash values reported by Schindler *et al.* (1971), and by Wissing and Hasler (1968, 1971) were obtained by the loss of weight following oxygen bomb combustion; therefore, their ash values are underestimates. The ash contents reported by Moshiri and Cummins (1969) were determined by direct ashing in a muffle furnace. However, their values were considerably lower than the ash values of *D. ambigua* (Table 8).

The calorific values of *D. ambigua* (cal/g dry wt and cal/g ash free dry wt), are in the range of values reported by other workers for other species of *Daphnia* (Table 8).

The significant correlations between both egg density and population density of *D. ambigua* and food concentration suggest that the seasonal trends in these population parameters generally were determined by food. In this study high food concentrations occurred during low temperatures. At low temperatures the time of egg development increased which decreased birth rate even though food concentration was high. This relationship probably explains why food concentration and instantaneous birth rates were not significantly related.

The disappearance of *D. ambigua* from the pond after June 12, 1973 could probably be attributed to the high respiratory expenditure of daphnids in response to high temperatures (Armitage and Lei, 1979) and to decreasing food. During this period the concentrations of chlorophyll *a* and seston were low (Fig. 1) and the population densities of *Ceriodaphnia* and *Diaptomus* were high (Lei, 1979). A bloom of *Aphanizomenon* sp. also occurred during this period; blue-green algae are a poor food source for zooplankters (Schindler, 1971, Arnold, 1971). Competition with colonial rotifers probably was significant. On several occasions we lost laboratory cultures of *Daphnia,* including *D. ambigua,* when a rotifer bloom developed in the culture.

High temperature and competition for food prevented daphnids from obtaining sufficient energy for both maintenance and reproduction and led to the complete disappearance of the population. However, the ability of *D. ambigua* to produce a high population and egg density in the cold season can be attributed to physiological adaptations. The filtering and respiratory rate-curves of cold-acclimatized

field daphnids showed classical translation when compared to the rate-curves of warm-acclimatized animals (Armitage and Lei, 1979). Acclimatization enables *D. ambigua* to maintain high activity and utilize the high food concentrations during the colder season.

Seasonal mean clutch size (2.01) of field *D. ambigua* obtained in this study is similar to the value reported for other populations of *D. ambigua* (1.97, Angino *et al.*, 1973; 1.67, Kwick and Carter, 1975) but is much lower than the value obtained for a laboratory population (Lei, 1979). Because the laboratory population had much higher food concentrations, the low mean clutch size of field animals probably resulted from the low food concentration in the field.

The brood size of *Daphnia* is positively correlated with the size of ovigerous females both in laboratory cultures (Anderson *et al.*, 1937; Anderson and Jenkin, 1942; Green, 1954; Richman, 1958; Buikema, 1973; Lei and Clifford, 1974; Vijverberg, 1976) and in field populations (Green, 1956; George and Edwards, 1974; Lei and Clifford, 1974). However, for the field population of *D. ambigua,* there was no consistent relationship between clutch size and size of females. Seemingly, the significant positive relationship between egg number and size of reproductive females occurs only under favorable nutritive conditions.

Clutch size and mean length of parthenogenetic females fluctuated together for populations of *D. magna* (Green, 1956) and *D. hyalina* (George and Edwards, 1974). But for populations of *D. schodleri* (Lei, 1968) and *D. ambigua* (Figs. 5 & 6), clutch size and the mean length of the parthenogenetic female did not fluctuate together. When environmental conditions, especially food concentration, change, a given-sized female may produce more eggs at one time than at another. Furthermore, under favorable food conditions, smaller females could produce more eggs than could larger females under poor food conditions. Therefore, the positive relationship between clutch size and the size of ovigerous females might not hold when considered over an entire season.

The positive correlation between parthenogenetic egg production and the estimate of food concentration is contrary to the negative correlation reported for *D. ambigua* in another pond in eastern Kansas (Angino *et al.*, 1973). They attributed the negative relationship to the grazing effect of reproducing females on the algal population. Parthenogenetic egg production of *D. ambigua* was negatively correlated with temperature (Table 3). Respiration increases at high temperatures (Armitage and Lei, 1979); probably less energy is available for egg production. However, in this study higher food concentration during the colder season might contribute to the negative relationship between egg production and temperature.

A very low average number of eggs per adult female is expected in an equilibrium population which has reached the carrying capacity of its environment in terms of the food supply. At equilibrium only one egg, on the average, will be produced by each animal; because the life expectancy of daphnids includes more than one reproductive instar, equilibrium brood size (eggs per adult female) must be less than one (Hall, 1964). The average brood size in an equilibrium, food-limited laboratory population of *Daphnia obtusa* was less than 0.5 eggs/adult (Slobodkin, 1954). In this study, the population of *D. ambigua* during most parts of June, July and September of 1972, and also most parts of March, May and part of April and June of 1973 probably was food limited and might have reached an equilibrium. During these time periods, the mean number

of eggs per adult female was less than one and on certain dates approached zero.

The larger size of the smallest reproductive females occurring during the cool season can be attributed to high food concentrations and low temperatures. Size of primiparia and maximum size of *Daphnia* are larger at high food concentration (Green, 1954; Richman, 1958; Hall, 1964; Weglenska, 1971) and low temperature (MacArthur and Baillie, 1929; Lei, 1968, 1979). The larger mean size and maximum size of reproductive females of *D. ambigua* occurring when temperatures were low resulted from the increased survival and continued growth of adult females. Larger size also may be associated with high food concentrations (Hall, 1964), low temperatures (MacArthur and Baillie, 1929), and low fish predation (Applegate and Mullan, 1969). Respiratory expenditure might be a key factor determining how large an animal can grow in a food-limited natural environment. Because respiration of *D. ambigua* increases with increasing body size and temperature (Armitage and Lei, 1979), the high respiratory rate of large individuals at high temperature could prevent large daphnids from obtaining enough energy for both growth and survival.

Theoretically, death rate (d′) can not be negative because a negative death rate means that the observed rate of population growth (r′) exceeds the potential rate of population growth (b′). Therefore, in real populations, negative death rates result from sampling error, immigration, or hatching of resting eggs (Edmondson, 1972). In this study, immigration may be eliminated because there was no source of immigrants. Therefore, the most probable cause is sampling error though hatching of resting eggs may have contributed to negative death rates. Negative death rates occurred frequently in a population of *Leptodora kindtii* and other prey populations (Cummins *et al.*, 1969). The common negative death rate in the population of *Daphnia retrocurva* in Sunfish Lake, Ontario was attributed, in part, to the hatching of ephippia (Clark and Carter, 1974).

More zero values occurred among the daily $P_g + P_r$ estimates calculated by the egg ratio method (ERM) than among those calculated by Winberg's method (WM) (Lei, 1979). Because, in ERM, production was calculated by multiplying the finite birth rate by standing crop biomass, the $P_g + P_r$ estimate was zero when birth rate was zero, even when the standing crop biomass was large. Because birth rate was estimated from egg numbers, the birth rate was zero when eggs were absent. The estimates of zero production on dates when eggs were absent but daphnids were present is probably unrealistic. Although there is no egg production (P_r), somatic production (P_g) probably results from the growth of individuals. Therefore, during the period when egg production was absent or extremely low, ERM probably underestimated production (e.g., June and July, 1972; June 1973). On the contrary, when egg production was high, ERM could overestimate production if the mortality of eggs was not considered. If eggs that are non-viable and/or lost with the death of ovigerous females are included in the calculation of birth rate, both birth rate and production will be overestimated. We do not know if the similarity of the results obtained for the whole study period by the two methods was fortuitous. If the similarity is real, then in a long term study (one growing season or one year) either of the two methods could be used to estimate production. However, in a short term investigation (e.g., one week or one month), production estimated by the two methods would be very different. Depending on the intensity of egg production in the

period studied, the values obtained by ERM would be either larger or smaller than the values obtained by WM.

The P/B coefficient of 25 for the period July 1972 to June 1973 is very close to the annual P/B coefficient reported for *Daphnia hyalina* (20.8 to 25.9, George and Edwards, 1974) and for a *Daphnia ambigua-parvula* complex (20.1 to 24.8) in Lake B (Geiling, 1969) but is lower than that reported for *Daphnia cucullata* (52.2, Petrovich *et al.*, 1961) and for the *D. ambigua-parvula* complex (58.6 to 68.0) in Lake D (Geiling, 1969).

A much shorter biomass turnover time of 3.8 days was obtained for the period July through August 1972. This short turnover time is close to that of 4 days for *Daphnia galeata mendotae* for the same months in Base Line Lake, Michigan (Hall, 1964).

Mean daily P/B coefficient and turnover time vary considerably among the same and/or different species of *Daphnia* in the same or different water bodies (Table 7). The daily P/B coefficient is equivalent to the turnover rate of biomass and reflects the reproductive capacity of a species under the conditions of its water body (Bekman and Menshutkin, 1964). Daily P/B coefficients for herbivorous planktonic crustaceans from lakes of different trophic types tended to increase in proportion to the productivity of a lake (Patalas, 1970); the lowest value for lakes in Byelorussia was 0.06 for mesotrophic Lake Naroch. Daily P/B for herbivorous planktonic crustaceans in a thermally polluted lake was twice as high as that of a similar but unpolluted lake (Patalas, 1970). However, Pederson *et al.* (1976) reported that the daily P/B coefficients of the zooplankton were not related to the trophic status of several lakes in Washington. Turnover time, depending on the method of estimation, is the reciprocal of turnover rate of number of individuals or of biomass, and is also indicative of conditions at which a species lives rather than the inherent characteristics of a species (Stross *et al.*, 1961). Therefore, the difference in the P/B coefficient and in the turnover time for populations of the same species may reflect differences in the temperature regimes (Hall, 1964) although nutrition (Weglenska, 1971) and other factors may also be involved. The differences in mean daily P/B coefficient and turnover time for *D. ambigua* seem to be related more to temperature than to nutrition (Table 7).

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TABLE 1

CALORIFIC VALUE OF *Daphnia ambigua* IN CALORIES PER GRAM OF DRY WEIGHT (OR CALORIES PER GRAM ASH FREE DRY WEIGHT) AS DETERMINED BY OXYGEN BOMB CALORIMETRY AND WET COMBUSTION METHOD.

	OXYGEN BOMB METHOD			WET COMBUSTION METHOD		
Analysis	Size I	Size III	Eggs	Size I	Size II	Size III
	(1)					
1	4381 (5.97)	4833 (10.51)	5227 (0.79)	3632 (1.05)	3949 (1.47)	4041 (0.84)
	(2)					
	5593	*5589*				
2	4356 (5.20)	4533 (6.70)	5135 (1.91)	3845 (2.38)	4001 (1.92)	4388 (1.67)
	5561	*5242*				
3		5067 (7.85)	5203 (1.77)	3830 (1.95)	3944 (1.80)	4242 (3.69)
		5860				
4		5130 (6.80)		3844 (2.00)	4079 (1.87)	4570 (1.20)
		5933				
5		5055 (5.98)		3988 (1.54)	4278 (2.48)	4348 (2.02)
		5846				
6					3943 (1.23)	4627 (1.70)
7					4094 (2.20)	
(1)						
Mean	4369	4924	5188	3828	4041	4369
Std. dev.	17.68	245.56	47.72	127.05	122.13	215.16
Coef. of Var.	0.4%	5.0%	0.9%	3.3%	3.0%	4.9%

(1) Calories per gram dry weight; the number in the parentheses is weight of sample (mg) used for determination.

(2) Calories per gram ash-free dry weight calculated on the basis of muffle furnace percent ash (see Table 2).

TABLE 2

ASH CONTENT (PERCENT OF DRY WEIGHT) OF *Daphnia ambigua*.

SIZE CLASS	EXP. NO.	DIRECT IGNITION (% ASH)	OXYGEN BOMB (% ASH)
I	1	21.31 (2.91)	16.26 (4.49)
	2	21.63 (2.50)	17.28 (5.34)
	3	22.08 (2.60)	15.22 (5.20)
	$\bar{x}$	21.67	16.25
	S.D.±	0.39	1.03
II	1	14.33 (3.49)	–
	2	18.47 (3.14)	–
	3	15.71 (3.50)	–
	4	9.30 (2.58)	–
	$\bar{x}$	14.45	–
	S.D.±	3.84	–
III	1	14.04 (4.70)	11.60 (10.51)
	2	13.10 (4.20)	8.87 (5.98)
	3	13.46 (3.79)	11.08 (6.70)
	4	–	11.68 (9.02)
	5	–	11.59 (7.85)
	6	–	11.84 (6.80)
	$\bar{x}$	13.53	11.11
	S.D.±	0.47	1.13

Number in Parentheses = weight of sample used (mg).

TABLE 3

THE CORRELATION BETWEEN PARTHENOGENETIC EGG PRODUCTION AND FOOD CONCENTRATION (SESTON IN CALORIES, CHLOROPHYLL *a* IN μG) AND TEMPERATURE.

Variables	r	n
Clutch size vs. seston/animal	0.345**	86
Number of eggs per adult ♀ vs. seston/animal	0.489***	91
Clutch size vs. seston/l	0.332**	86
Number of eggs per adult ♀ vs. seston/l	0.452***	91
Clutch size vs. chl. *a*/animal	0.601***	86
Number of eggs per adult ♀ vs. chl. *a*/animal	0.356**	91
Clutch size vs. chl. *a*/l	0.606***	86
Number of eggs per adult ♀ vs. chl. *a*/l	0.321**	91
Clutch size vs. temperature	−0.432**	86
Number of eggs per adult vs. temperature	−0.282*	91

n = sample size, *$p \leq 0.05$; **$p \leq 0.01$; ***$p \leq 0.001$.

TABLE 4

POPULATION DATA FOR *Daphnia ambigua* IN THE FISH LABORATORY POND.

DATE	MEAN TEMP. (C)	STANDING CROP: NO. PER LITER	STANDING CROP: MG PER M^3	STANDING CROP: CALORIES PER M^3	MEAN CLUTCH SIZE	EGGS PER ADULT ♀	EGGS PER LITER (E)	DEVELOPMENT TIME (DAYS) (D)	FINITE BIRTH RATE (B)	INSTANTANEOUS BIRTH RATE (b′)	POPULATION CHANGE RATE (r′)	TURNOVER TIME (DAYS) (T)	INSTANTANEOUS DEATH RATE (d′)
1972													
Jun 3	25.0	2.48	9.46	44.0	–	0	0	–	0	0	−1.467	–	1.467
5	25.2	0.13	0.60	2.8	–	0	0	–	0	0	–	–	–
7	26.0	0	0	0	–	–	0	–	–	–	–	–	–
9	26.4	0	0	0	–	–	0	–	–	–	–	–	–
11	26.2	0.05	0.07	0.3	–	–	0	–	0	0	–	–	–
13	25.9	0	0	0	–	–	0	–	–	–	–	–	–
15	25.0	0.03	0.04	0.2	–	–	0	–	0	0	0.187	–	−0.187
18	23.5	0.06	0.06	0.3	–	–	0	–	0	0	1.065	–	−1.065
21	23.2	1.37	3.81	18.6	3.30	1.86	0.44	1.89	0.1243	0.149	−0.374	8.1	0.523
23	24.5	0.65	1.58	7.5	2.65	0.33	0.03	1.74	0.0270	0.028	−0.076	37.0	0.104
28	25.3	0.44	0.65	2.9	–	–	0	–	0	0	1.943	–	−1.943
29	25.1	3.09	4.78	21.4	–	–	0	–	0	0	0.210	–	−0.210
Jul 1	24.8	4.70	8.21	37.0	–	0	0	–	0	0	0.036	–	−0.036
3	24.5	5.04	13.35	62.8	2.0	0.40	0.35	1.74	0.0383	0.038	0	26.1	0.038
5	24.2	0	0	0	–	–	0	–	–	–	–	–	–
9	24.6	0.03	0.12	0.6	–	0	0	–	0	0	−0.137	–	0.137
11	25.4	0.02	0.09	0.5	–	0	0	–	0	0	0.385	–	−0.385
13	25.9	0.04	0.05	0.2	–	–	0	–	0	0	−0.115	–	0.115
16	26.2	0.03	0.11	0.5	–	–	0	–	0	0	–	–	–
19	27.7	0	0	0	–	–	0	–	–	–	–	–	–
23	28.7	0	0	0	–	–	0	–	–	–	–	–	–
25	28.2	0	0	0	–	–	0	–	–	–	–	–	–
27	27.9	0.03	0.07	0.3	–	–	0	–	0	0	1.246	–	−1.246
29	27.5	0.30	1.13	5.4	2.08	2.08	0.09	1.49	0.1514	0.175	−0.296	6.6	0.471
31	27.2	0.17	0.33	1.5	–	–	0	–	0	0	0.418	–	−0.418
Aug 2	26.4	0.39	1.90	9.8	2.30	2.30	0.44	1.57	0.5797	0.489	0.332	1.7	0.157
7	25.9	2.02	9.93	49.8	2.83	1.62	1.57	1.61	0.3208	0.357	−0.220	3.1	0.577
8	26.4	1.62	9.15	46.7	2.86	2.39	1.94	1.57	0.4863	0.501	−0.061	2.1	0.563
10	28.0	1.44	7.07	35.2	2.23	1.41	0.87	1.45	0.2433	0.327	−0.623	4.1	0.950
14	29.3	0.12	0.15	0.7	–	–	0	–	0	0	0.647	–	−0.647
16	29.5	0.43	1.39	7.0	1.66	1.66	0.24	1.37	0.4493	0.322	0.635	2.2	−0.313
18	29.7	1.55	6.69	33.6	2.20	2.20	1.25	1.36	0.5830	0.436	0.555	1.7	−0.118
20	29.8	4.68	16.79	84.3	3.43	3.11	3.57	1.36	0.7790	0.418	1.140	1.3	−0.723
22	27.1	45.8	147.77	717.4	2.14	1.65	15.2	1.51	0.1723	0.197	−0.274	5.8	0.471
26	24.4	15.3	60.41	295.4	3.19	1.66	7.34	1.75	0.2213	0.224	−0.021	4.5	0.244
28	24.4	14.71	51.39	246.9	1.00	0.86	3.33	1.75	0.1531	0.117	0.524	6.5	−0.407
30	24.4	41.94	144.19	689.6	1.00	0.92	8.60	1.75	0.0967	0.107	−0.197	10.3	0.304
Sep 2	24.2	23.23	67.9	318.6	1.00	0.20	0.90	1.77	0.0163	0.022	−0.583	61.4	0.605
5	23.9	4.04	15.57	74.7	1.00	0.06	0.11	1.81	0.0147	0.015	−0.045	67.9	0.060
11	23.6	3.08	15.67	78.9	1.38	1.38	2.27	1.84	0.4106	0.300	0.600	2.4	−0.300
14	23.7	18.62	67.55	326.7	1.47	1.06	5.39	1.83	0.1301	0.139	−0.133	7.7	0.272
15	23.7	16.29	61.64	298.4	1.47	1.05	4.72	1.83	0.1284	0.139	−0.163	7.8	0.302
17	23.8	11.76	45.95	225.6	1.42	0.91	4.28	1.82	0.1876	0.171	0.183	5.3	−0.012
21	23.4	24.46	84.63	404.3	1.00	0.36	2.58	1.86	0.0478	0.054	−0.243	20.9	0.297
23	22.8	15.04	63.59	306.2	1.00	0.53	2.88	1.94	0.0903	0.090	0.002	11.1	0.089
25	21.9	15.08	64.04	306.6	1.00	0.22	1.39	2.07	0.0461	0.043	0.151	21.7	−0.108
27	21.0	20.40	85.19	407.3	1.00	0.04	0.36	2.21	0.0072	0.008	−0.178	138.1	0.186
30	19.7	11.97	45.83	218.2	1.00	0.23	0.82	2.46	0.0259	0.027	−0.083	38.6	0.110
Oct 3	18.5	9.34	43.71	212.7	1.00	0.29	1.43	2.72	0.0510	0.052	−0.051	19.6	0.103
5	17.0	8.44	40.11	196.5	1.00	0.52	2.19	3.13	0.0710	0.074	−0.075	14.1	0.148
8	15.3	6.75	33.24	164.0	1.14	0.49	2.00	3.72	0.1172	0.070	0.961	8.5	−0.891
10	14.0	46.12	193.59	945.3	1.29	0.54	11.03	4.28	0.0383	0.050	−0.567	26.1	0.617
12	11.6	14.84	68.90	338.6	1.42	0.95	6.16	5.67	0.0617	0.061	0.015	16.2	0.046

TABLE 4 (Continued)

DATE		MEAN TEMP. (C)	STANDING CROP NO. PER LITER	STANDING CROP MG PER M^3	STANDING CROP CALORIES PER M^3	MEAN CLUTCH SIZE	EGGS PER ADULT ♀	EGGS PER LITER (E)	[illegible]	[illegible] BIRTH (AE)	[illegible] BIRTH (AE)	[illegible]	[illegible] (DAYS)	INSTANTANEOUS DEATH RATE (d)
	17	10.3	16.0	73.65	365.0	1.91	1.37	8.93	6.68	0.0690	0.066	0.074	14.5	−0.007
	26	10.4	31.07	150.91	744.5	1.50	1.05	14.52	6.59	0.0567	0.078	−0.052	17.6	0.110
Nov	1	9.2	22.77	103.74	518.1	1.57	1.54	14.17	7.72	0.0625	0.063	−0.005	16.0	0.068
	7	6.4	22.10	100.94	498.2	1.75	1.41	11.58	11.48	0.0372	0.037	0.025	26.9	0.011
	14	4.6	26.39	144.74	731.7	2.30	1.98	24.27	15.11	0.0432	0.043	0.002	23.1	0.041
	26	4.4	27.10	144.48	738.4	3.30	3.30	33.65	15.59	0.0526	0.052	0.032	19.0	0.020
Dec	15	4.8	49.59	483.78	2574.5	5.72	5.13	164.36	14.64	0.1022	0.100	0.047	9.8	0.053
1973														
Jan	10	5.1	168.42	1598.07	8399.8	5.03	5.03	471.10	13.98	0.0863	0.096	−0.206	11.6	0.302
	15	5.1	60.01	185.90	903.7	5.22	3.05	23.52	13.98	0.0235	0.024	−0.013	42.5	0.037
	25	5.0	52.64	196.31	959.3	4.80	1.65	22.35	14.19	0.0245	0.025	−0.038	40.9	0.063
Feb	5	5.0	34.53	209.97	1063.6	4.79	2.21	36.01	14.19	0.0519	0.050	0.059	19.3	−0.009
	14	5.0	58.86	285.95	1416.0	4.33	1.68	34.03	14.19	0.0344	0.032	0.132	29.1	−0.010
	22	5.6	168.68	795.96	3940.6	3.76	1.63	98.87	12.94	0.0356	0.036	−0.002	28.1	0.037
Mar	2	6.5	166.37	825.73	4076.2	3.96	1.86	98.11	11.31	0.0390	0.041	−0.100	25.6	0.141
	7	7.2	100.79	458.88	2249.0	3.21	1.58	46.06	10.21	0.0387	0.037	0.096	25.8	−0.059
	12	7.8	162.90	574.19	2750.1	2.19	1.12	32.80	9.37	0.0162	0.020	−0.391	61.1	0.410
	14	8.0	74.60	272 0	1297.2	1.94	0.74	12.22	9.11	0.0163	0.017	−0.039	61.2	0.056
	16	8.2	68.98	315.07	1519.6	1.43	0.52	11.76	8.86	0.0180	0.018	0.019	55.7	−0.001
	18	8.5	71.68	287.33	1364.8	1.46	0.37	6.54	8.49	0.0113	0.010	0.180	88.8	−0.170
	20	8.7	102.81	448.18	2153.9	1.55	0.39	13.57	8.26	0.0139	0.015	−0.154	71.9	0.169
	22	8.9	75.60	343.30	1642.8	1.63	0.59	13.07	8.04	0.0187	0.020	−0.122	53.6	0.142
	24	9.3	59.24	299.37	1452.0	1.97	0.71	15.61	7.62	0.0322	0.031	0.098	31.0	−0.067
	26	9.4	72.04	365.67	1784.2	1.85	0.59	20.55	7.52	0.0306	0.033	−0.177	32.7	0.211
	28	9.3	50.54	229.54	1115.6	1.68	0.46	9.69	7.62	0.0237	0.023	0.057	42.2	−0.034
	31	9.1	60.03	334.47	1662.7	1.69	0.80	28.13	7.83	0.0478	0.049	−0.054	20.9	0.103
Apr	3	8.8	51.12	277.33	1373.4	1.55	0.71	20.67	8.15	0.0473	0.042	0.251	21.1	−0.209
	5	8.6	84.38	482.34	2401.8	1.71	0.93	44.85	8.38	0.0424	0.051	−0.375	23.6	0.426
	7	8.4	39.83	255.24	1292.8	2.32	1.76	36.71	8.61	0.0768	0.076	0.025	13.0	0.051
	9	8.2	41.83	223.99	1114.2	2.36	1.77	27.50	8.86	0.0720	0.057	0.447	13.9	−0.390
	11	8.7	102.35	486.50	2410.4	2.88	2.17	65.96	8.26	0.0649	0.060	0.149	15.4	−0.088
	13	9.7	137.73	481.40	2300.9	3.03	1.44	34.07	7.22	0.0327	0.031	0.132	30.6	−0.102
	16	10.5	204.84	797.58	3862.9	3.50	1.22	63.55	6.51	0.0385	0.042	−0.155	26.0	0.196
	18	11.6	150.39	636.14	3111.5	3.33	2.19	76.38	5.81	0.0711	0.071	0.010	14.1	0.061
	22	12.8	156.54	661.94	3244.5	2.53	0.90	31.54	4.91	0.0441	0.037	0.322	22.7	−0.284
	24	14.0	297.78	996.98	4763.8	1.39	0.60	24.21	4.28	0.0186	0.018	0.035	53.8	−0.017
	26	14.7	319.64	1111.87	5265.5	1.08	0.22	18.45	3.96	0.0113	0.014	−0.469	88.4	0.483
	28	15.0	125.24	424.57	1991.5	1.06	0.14	4.48	3.84	0.0083	0.009	−0.192	120.0	0.201
	30	15.2	85.29	265.07	1231.8	1.20	0.07	1.10	3.76	0.0030	0.003	−0.303	338.9	0.306
May	1	15.4	63.01	220.32	1030.9	1.00	0.10	1.44	3.68	0.0068	0.006	0.205	146.9	−0.199
	4	15.9	116.45	439.51	2068.1	1.35	0.38	10.51	3.49	0.0238	0.025	−0.075	42.0	0.100
	6	16.4	100.22	418.70	2002.6	1.24	0.78	23.32	3.32	0.0569	0.063	−0.207	17.6	0.270
	8	16.7	66.32	275.24	1335.0	1.25	0.78	19.44	3.23	0.0841	0.080	0.106	11.9	−0.026
	11	16.9	91.09	329.43	1609.4	1.38	1.12	34.14	3.16	0.1074	0.101	0.129	9.3	−0.028
	12	17.2	103.61	344.77	1653.1	1.32	0.79	21.67	3.07	0.0548	0.062	−0.247	18.3	0.309
	14	17.4	63.18	210.53	995.5	1.23	0.38	5.23	3.01	0.0213	0.026	−0.445	46.9	0.471
	16	17.3	25.97	104.02	501.8	1.40	0.71	6.59	3.04	0.0950	0.074	0.473	10.5	−0.399
	18	18.1	66.90	300.07	1475.5	1.24	0.97	30.09	2.82	0.1147	0.132	−0.280	8.7	0.411
	20	19.2	38.24	177.84	894.6	1.61	1.41	26.83	2.56	0.2512	0.207	0.372	4.0	−0.164
	24	19.3	168.97	808.14	4020.5	1.79	1.53	117.92	2.54	0.1950	0.208	−0.135	5.1	0.343
	26	19.3	129.08	474.64	2306.9	1.26	1.05	41.69	2.54	0.1017	0.110	−0.163	9.8	0.273
	29	19.6	79.24	295.71	1415.2	1.05	0.32	8.56	2.48	0.0404	0.041	−0.053	24.8	0.094
	31	20.0	71.30	252.88	1183.4	1.00	0.11	1.85	2.40	0.0108	0.011	0.028	92.3	−0.017
Jun	2	20.3	75.41	366.11	1777.7	1.01	0.49	17.72	2.34	0.0954	0.090	0.110	10.5	−0.020
	4	20.7	93.95	383.94	1839.2	1.00	0.27	9.42	2.26	0.0410	0.042	−0.055	24.4	0.097

TABLE 4 (Continued)

Date	Mean temp. (C)	Standing crop: No. per liter	Standing crop: mg per m^3	Standing crop: Calories per m^3	Mean clutch size	Eggs per adult ♀	Eggs per liter (E)	Development time (days) (D)	Finite birth rate (B)	Instantaneous birth rate (b′)	Population change rate (r′)	Turnover time (days) (T)	Instantaneous death rate (d′)
6	21.3	84.18	331.82	1579.1	1.00	0.01	0.44	2.16	0.0025	0.002	0.068	404.3	−0.065
8	21.9	96.35	423.49	2036.8	–	0	0	–	0	0	−1.273	–	1.273
10	22.9	7.55	23.49	109.5	–	0	0	–	0	0	−1.589	–	1.589
12	23.6	0.32	0.68	3.0	–	–	0	–	0	0	–	–	–
14	23.5	0	0	0	–	–	0	–	–	–	–	–	–

TABLE 5

MONTHLY AND ANNUAL MEAN BIOMASS AND PRODUCTION ($P = P_g + P_r$) FOR *D. ambigua*. VALUES OF P ARE THE MEANS OF THE ESTIMATES PROVIDED BY THE EGG RATIO AND WINBERG METHODS. MONTHLY VALUES OF P OF RESTING EGGS SHOWN SEPARATELY IN PARENTHESES. PRODUCTION OF RESTING EGGS IS INCLUDED IN THE ANNUAL VALUES OF P.

	Mean Biomass ($\bar{B}$)		Production (P)		P/B Coefficient	
	mg dry wt/m^3	cal/m^3	mg dry wt/m^3	cal/m^3	mg/mg	cal/cal
1972						
June	1.8	8.2	8.1	37.4	4.6	4.5
July	1.8	8.4	6.9	32.1	3.8	3.8
Aug.	38.1	184.7	291.5	1428.7	7.7	7.7
Sep.	56.1	269.6	202.8	997.8	3.6	3.7
Oct.	86.3	423.8	184.3	914.8	2.1	2.2
Nov.	123.5	621.6	183.9	946.7	1.5	1.5
Dec.	483.8	2574.5	1273.8	6845.8	2.6	2.7
1973						
Jan.	660.1	3420.9	1165.5	6179.8	1.8	1.8
Feb.	430.6	2140.1	469.3	2355.6	1.1	1.1
Mar.			(0.29)	(1.7)		
	396.1	1922.3	466.7	2280.0	1.2	1.2
Apr.			(65.7)	(386.6)		
	546.2	2643.5	903.3	4370.1	1.8	1.8
May			(0.43)	(2.5)		
	332.3	1606.6	1296.4	6395.1	3.9	4.0
June	109.3	524.7	233.9	1105.5	2.1	2.1
1972 June to 1973 June	251.2	1257.6	6753.0	34279.9	26.9	27.3
1972 July to 1973 June	272.0	1361.7	6744.8	34242.6	24.8	25.1

TABLE 6

MONTHLY PRODUCTION AND TOTAL PRODUCTION FOR *D. ambigua*. RESTING EGGS NOT INCLUDED. ERM = EGG RATIO METHOD, WM = WINBERG'S METHOD.

	PRODUCTION				
	$P_g + P_r$				P_{ex}
	ERM		WM		
Date	mg/m³	cal/m³	mg/m³	cal/m³	cal/m³
1972					
June	1.3	6.5	14.9	68.2	19.9
July	1.6	7.8	12.2	56.3	18.3
August	226.1	1106.8	356.9	1750.6	504.2
September	126.0	659.3	279.7	1336.2	576.9
October	171.7	847.3	197.0	982.2	382.8
November	214.4	1092.8	153.4	800.5	200.0
December	1808.5	9566.0	739.0	4125.5	641.6
1973					
January	1551.6	8125.9	779.3	4233.7	794.3
February	495.3	2460.1	443.4	2251.1	729.2
March	380.6	1860.7	552.7	2699.3	1147.9
April	627.3	3071.0	1179.4	5669.3	2384.9
May	1101.3	5419.5	1491.5	7370.6	2752.8
June	95.0	458.8	372.8	1752.2	1058.8
June 1972-June 1973	6800.8	34682.5	6572.3	33095.7	11211.8
July 1972-June 1973	6799.4	34676.0	6557.4	33027.4	11191.8

TABLE 7

COMPARISON OF MEAN BIOMASS, MEAN DAILY PRODUCTION, MEAN DAILY P/B, AND MEAN TURNOVER TIME FOR SEVERAL SPECIES OF *Daphnia*.

SPECIES	MEAN BIOMASS ($\bar{B}$)	MEAN DAILY PRODUCTION	MEAN DAILY P/B	MEAN TURN-OVER TIME (DAYS)	PERIOD OF STUDY	MEAN WATER TEMP. (C°)	MEAN SESTON CONC. (CAL/L)	SOURCE
D. schödleri	1.568 g/m²	0.227 g/m²	0.145	6.9	Apr~Sep 1958			Wright (1965)
D. galeata mendotae	1.114	0.114	0.10	10.0	Apr~Sep 1958			Wright (1965)
D. cucullata and *D. longispina hyalina*	0.950 g/m²	0.128 g/m²	0.135	7.4[1]	Jul~Aug 1966	21.6		Patalas (1970)
	5.497	1.547	0.281	3.6[2]	Jul~Aug 1966	27.4		Patalas (1970)
D. hyalina	0.570 g/m²	0.027 g/m²	0.047	21.3	Jan~Dec 1970			George and Edwards (1974)
	0.320	0.020	0.063	15.9	Jan~Dec 1971			
D. cucullata	1.690 g/m³	0.337 g/m³	0.199	5.0	Jul~Aug 1964	19.5		Hillbricht-Ilkowska & Weglenska (1970)
D. ambigua-parvula complex	0.478 g/m²	0.048 g/m²	0.100	10.0[3]	Mar~Nov 1965			Geiling (1969)
	0.367	0.037	0.100	10.0[3]	Mar~Nov 1966			
	0.064	0.016	0.250	4.0[4]	Mar~Nov 1965			
	0.117	0.028	0.239	4.2[4]	Mar~Nov 1966			
D. galeata mendotae		0.407 g/m³			May~Nov 1966	15.0		Cummins et al (1969)
		0.030			May~Nov 1967	14.0		

TABLE 7 (Continued)

D. cucullata	0.064 g/m^3	0.016 g/m^3	0.25	4.0	Apr~Nov	1960	13.5		Petrovich et al. (1961)
D. ambigua				5-6	May~Nov	1974			Kwick and Carter (1975)
D. ambigua	0.019 g/m^3	0.005 g/m^3	0.263	3.8	Jul~Aug	1972	26.7	10.1	Present study
	0.038	0.004	0.105	9.5	Jun~Nov	1972	22.8	15.4	
	0.272	0.018	0.066	15.2	Jul 1972~ Jun 1973		17.3	16.6	
	0.251	0.017	0.068	14.7	Jun 1972~ Jun 1973		18.1	15.7	
	0.361	0.025	0.069	14.5	Jan~Jun	1973	12.9	13.4	
D. galeata mendotae		0.009 g/m^3			Jul~Aug	1966	23.0		Cummins et al. (1969)
		0.005 g/m^3			Jul~Aug	1967	22.7		
D. galeata mendotae				4.0	Jul~Aug	1961			Hall (1964)
D. longispina				14.7	Jun~Sep	1956			Stross et al. (1961)
D. pulex				32.2	Jun~Sep	1956			
D. longispina	2.390 g/m^3	0.360 g/m^3	0.15	6.7[5]	Jun~Oct	1967	25.8		Lewkowicz (1971)
	2.480	0.48	0.19	5.3[6]					
	2.450	0.53	0.21	4.7[7]					
D. cucullata	0.6 g/m^3	0.057 g/m^3	0.095	10.5[8]	May~Sep	1962			Winberg et al. (1965)
	0.7	0.064	0.091	11.0[9]	May~Sep	1962			
	0.4	0.009	0.087	11.5[10]	May~Sep	1960			
D. cristata			0.31	3.2[11]		1968			Winberg (1972)
			0.29	3.4[11]		1969			
			0.23	4.3[12]		1968			
			0.16	6.2[12]		1969			

[1] Lake Mikorzynskie (no thermal effluents).
[2] Lake Lickenskie (receives thermal effluents).
[3] Lake B of a series of stripmine lakes in Missouri.
[4] Lake D of a series of stripmine lakes in Missouri.
[5] Carp pond (unfertilized).
[6] Carp pond (fertilized with phosphorus fertilizer).
[7] Carp pond (fertilized with phosphorus and nitrogen).
[8] Lake Batorin (Eutrophic).
[9] Lake Myastro (Mesotrophic).
[10] Lake Naroch (Oligotrophic).
[11] Lake Krivoe.
[12] Lake Krugloe.

TABLE 8

CALORIFIC VALUES OF *Daphnia* SPECIES.

SPECIES	SPECIFICATION	METHOD	CAL/G DRY WT	% ASH	CAL/G ASH-FREE DRY WT	REFERENCE
Daphnia magna	—	C	3694	33.17	4988	Ivlev (1934)
Daphnia magna	—	C	3700	—	4967	Fischer, unpublished (after Prus, 1970)
Daphnia magna	Mix eggless and with egg	B	5640±60	7.4±0.2	5898±63	Moshiri & Cummins (1969)
Daphnia magna	1.0~2.5mm	B	4852~4925	—	—	Schindler (1968)
Daphnia pulex	juvenile	W	4330	—	—	Pecken & Kuznetsova (1966)
	♀ ♀ with eggs	W	4640	—	—	Pecken & Kuznetsova (1966)
Daphnia pulex	—	C	4365	18.25	5674	Ivlev (1934) (after Prus, 1970)
Daphnia pulex	0.7, 1.3, 1.8mm	B	4419	—	5362	Richman (1958)
Daphnia pulex	juvenile	C	4141	17.6	—	Birge and Juday (1920) (after Richman, 1958)
	reproductive animal	C	5350			Birge and Juday (1920) (after Richman, 1958)
Daphnia pulex	1.92mm	B	4478±372	—	—	Comita and Schindler (1963)
Daphnia galeata mendotae	eggless	B	5118±89	7.7±0.2	5511±85	Moshiri and Cummins (1969)
	with eggs	B	5372±54	8.3±2	5817±58	Moshiri and Cummins (1969)
	eggs only	B	5850	4.0	6098	Moshiri and Cummins (1969)
Daphnia dubia	—	B	4767	8.36	5331	Schindler, *et al.* (1971)
Daphnia spp.	—	B	4630 (4170~5115)	8.99 (5.9~13.0)	5030 (4648~5395)	Wissing & Hasler (1971)
Daphnia spp.	—	B	—	9.78 (5.5~13.4)	5006 (4132~5643)	Wissing & Hasler (1969)
	females with eggs	B	4532 (3776~5652)	6.28 (3.8~9.0)	—	Wissing & Hasler (1969)
Daphnia pulicaria	mean of all size groups (1.1~3.1mm)	B	5399*	—	—	Snow (1972)
Daphnia ambigua	<0.62mm (carapace length)	B	4369±18	21.67	5578±23	Present Study
	0.62~0.87mm (carapace length)	W	4583±139	14.45	5357±162	Present Study
	>0.87mm (carapace length) (adult) eggs only	B	4924±246	13.53	5694±285	Present Study
		W	5883±54	—	—	Present Study

B-Bomb Calorimetry.
C-Chemical Composition.
W-Wet Combustion.
*-Mean of all size groups in Table 2 of Snow (1972).

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